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PREDICTING CROP PHENOLOGY

Tom Hodges

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Chapter 1

INTRODUCTION

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Phenology refers to the development, differentiation, and initiation of organs. Growth refers to accumulation of biomass in the plant as a whole or in certain organs. This book, *Predicting Crop Phenology*, focuses on the use of crop growth simulation models to predict the development of crops. Accurate prediction of crop development patterns will assist farm managers in growing crops so that the most critical stages of growth occur during periods of favorable weather. The act of developing crop phenology models also results in improved understanding of crop development and growth processes. Another book or several books would be needed to address the topic of predicting crop growth and yield, so these issues are not dealt with here except as they relate to phenology.

For the purposes of this book, a model or crop growth simulation model refers to a computer program that simulates the response of the major plant physiological processes to environmental factors and to each other. Broader definitions of a model could include any algorithm (quantitative statement) to predict the response of a process to its environment or even any theory (qualitative statement) about how a process responds to its environment.

The organization of the book is as follows. The nature of crop simulation modeling and its role in agriculture is discussed. The importance of phenological modeling in crop growth simulation modeling is explained. Then the major factors controlling plant phenological responses (temperature, daylength, and vernalization) and the types of phenological response are discussed, as is water stress. Plant phenological responses include vernalization and leaf, stem, root, and tiller development. Flowering and seed growth have been discussed in many excellent review articles so they will not be treated separately here.[1-7] Issues in computer programming techniques are discussed in relation to crop simulation modeling. These issues include mechanistic vs. empirical models, research vs. application models, structured and top-down programming, and libraries of reusable subroutines. Specific models for wheat, maize, sorghum/millet, cotton, legumes, and rice are discussed in terms of how modelers have addressed the prediction of phenological processes, including the reproductive processes.

A note for those who are not conversant with computer programming languages: many of the equations in the chapters about specific models are actually instructions from computer programs. There is a fundamental difference between the mathematical equation A = B and the same statement in a computer program in almost any of the programming languages. In mathematics, it is a statement of equality or equivalence. In a computer program, it is an instruction to calculate the value of the expression to the right of the equal sign and put it in the variable on the left side of the equal sign. Thus, mathematically, A = A + 1 is nonsensical, but as a computer instruction it is a very common way to increase A in value by 1. Many of the equations in the book will make sense only if read as instructions rather than as mathematical equations.

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Chapter 2

CROP GROWTH SIMULATION AND THE ROLE OF PHENOLOGICAL MODELS

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I. THE ROLE OF MODELING RESEARCH IN CROP PRODUCTION

A. INTEGRATING KNOWLEDGE

Modeling is a means of integrating knowledge from various scientific disciplines into a coordinated whole. If our understanding of biological and environmental processes can be expressed in quantitative terms, i.e., mathematically, then growth and development processes, their interactions with each other, and their interactions with the environment can be combined in a computer program or model. Such a model can be used to predict the growth and development of a biological system under a variety of environments.[1] A biological system might range from a detached leaf carrying on photosynthesis and respiration, to a plant growing in a growth chamber under strictly controlled conditions, to a series of crops being rotated in a field over several years with microorganisms, weeds, insects, soil, weather, and management factors affecting growth and development.

In agriculture, models have been developed for numerous components of cropping systems, such as specific crops, insects, weeds, diseases, and soil processes. These models are based on quantitative theories of how physical and biological processes respond to their environment and to each other. Scientists are now beginning to combine some of these component models into larger models of complex cropping systems.

B. TESTING QUANTITATIVE HYPOTHESES

Quantitative hypotheses of the mode of interaction between different processes in a system can be tested in models.

When a hypothesis is implemented in a model, unreasonable model results may invalidate the hypothesis or lead to new understanding of the conditions under which a process operates. Unreasonable results may also be due to incorrect implementation of the hypothesis in the model.

Examples of processes for which hypothesis might be tested are

1. Rate of new tiller appearance on wheat plants as a function of temperature and the net photosynthetic rate minus the rate of carbohydrate use for shoot and root growth.
2. Partitioning of carbohydrate to shoot and root during vegetative growth as a function of degree of water and nitrogen stress and air and soil temperatures.

C. TECHNOLOGY TRANSFER

Knowledge can be incorporated into a computer program or crop growth simulation model and transferred to any user who can use the information to solve practical problems and make decisions. With the widespread availability of increasingly powerful microcomputers running the Microsoft or other widely used operating systems, computer programs can be readily transferred to extension offices, agricultural consultants, or directly to farm managers anywhere in the world merely for the cost of postage. However, for effective technology transfer, programs must meet certain minimum requirements.

1. The program must be usable by the people who are expected to benefit from it. If a great deal of experience in using microcomputers or advanced academic knowledge of agricultural science is required to effectively use a program, then a relatively small body of users will be able to benefit from the program.
2. The program must require only the data that users will be able to acquire with a level of effort and expense commensurate with the anticipated benefit to be derived from using the model.
3. The program must provide accurate information applicable to the class of problems or decisions for which it is intended.

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II. IMPORTANCE OF PHENOLOGICAL MODELING IN CROP GROWTH MODELING

A portion of a crop growth simulation model must be devoted to predicting the timing of crop growth processes (phenology). Without accurate prediction of phenology, the model will simulate growth processes as occurring at different times and under different conditions than they actually do. In some models, phenological predictions may be intertwined among many other parts of the computer program, but in many models, phenological functions are in a separate section of the program, where they can be modified or replaced without fundamental changes to the rest of the program.

Accurate prediction of the timing of growth stages is essential to the prediction of physiological responses under varying conditions, i.e., under field conditions. Conditions during each growth stage affect the ability of the crop to respond to conditions during later stages.[2-5]

As temperature, moisture, daylength, light, and other environmental factors change through the growing season, the model must accurately predict when each growth process will begin and end.

The following examples illustrate the importance of predicting growth stage accurately:

1. Pesticides must frequently be applied at certain growth stages of the crop or the pest.
2. Stress during flowering or grain filling will have a great effect on grain yield, whereas stress during vegetative growth will often have very little effect.
3. Global changes in climate due to increasing concentration of CO_2 and other greenhouse gases will require changes in phenological responses to the environment via new crop varieties or new crop types, in order to make optimal use of evolving changes in local climates.

A. ANNUALS

In many regions, growth of annual crops must occur between episodes of drought, heat, or cold.[6] For optimum yields, it is essential that varieties and planting dates be selected so that stages critically affecting economic yield will occur during periods of optimum growing conditions[7] and so that full use will be made of these periods. Interactions between developments during each stage must also be considered.[3,4,8] Sufficiently severe stress during any stage can adversely affect crop yields.[9]

B. PERENNIALS

For perennial crops, timing of growth stages determines availability of stored materials, periods when stored materials will be consumed or accumulated, the conditions under which economic yield will be produced, the effects of periodic harvests on regrowth, and the beginning and end of periods of dormancy. The timing of growth stages also determines whether a species will survive in a region with periods of extremely unfavorable conditions, such as heat, cold, flooding, or drought.

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Chapter 3

TEMPERATURE AND WATER STRESS EFFECTS ON PHENOLOGY

Tom Hodges

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I. INTRODUCTION

A primary factor affecting crop development is temperature, as modulated by other factors including daylength, vernalization, heat and cold stress, and water stress. The rate of change of daylength may also have an effect on development independent of daylength.[1] The temperature experienced by the plant may be thought of as an empirical analog for the amount of "physiological time" that the plant has experienced. Modelers have attempted to assess quantitatively the effects of temperature by calculating accumulated thermal time, i.e., the total effective temperature to which a plant has been exposed. Relationships have been found to vary in form from simply linear to variously nonlinear and to be generally quite limited and specific as to site and plant material. This can be expected since most relationships are descriptive rather than based on underlying processes. Plants at different growth stages, different crop species, and different varieties or cultivars within a species have different responses to temperature and the other modulating factors.

Thermal time is typically based on air temperature except during early growth when meristems are still below or near the ground. At such stages, it may be most appropriate to use soil temperature rather than air temperature to accumulate thermal time.[2] Swan et al.[3] reported that management of the residue from the previous crop affected the response of maize to temperature, probably because of the influence of the residue on soil temperature.

II. TEMPERATURE

A. THERMAL TIME ACCUMULATION

The effect of temperature or thermal time accumulation on crop growth and development has recently been reviewed by Ritchie and NeSmith.[4]

The basic concept of thermal time is as follows.[5,6] Many crop phenological and growth processes proceed in direct relation to the accumulated temperature or thermal time experienced by the crop. Below a base temperature, no thermal time accumulates and crop development ceases. The rate of thermal time accumulation and the crop growth or development rate increase with increasing temperature up to an optimum temperature value or range of values (plateau). Above that temperature value or plateau the rate of thermal time accumulation and the crop response decrease with further increases in temperature until no further accumulation occurs and crop development ceases[7,8] (Figure 1). Various linear[9,10] and nonlinear[11-14] algorithms have been developed to calculate the accumulated thermal time that a crop experiences. Wassink[14] shows how some exponential functions may generate a nearly linear response over part of a range, while being curvilinear over other parts. Innumerable greenhouse, growth chamber, and field studies have been carried out in an attempt to determine the cardinal (minimum, optimum, and maximum) temperatures for development in the several stages of different varieties of many crops. Studies and reviews include those by Barlow et al.,[15] and Boersma,[15] Bunting,[16] Cross and Zuber,[10] Frank et al.,[17] Hesketh et al.,[18] Hodges,[19] Hodges and French,[20] Major and Johnson,[7] Major et al.,[13] Ritchie and NeSmith,[4] and Warrington and Kanemasu.[21,22]

For soybean,[20,23] maize,[24,25] and wheat,[26] thermal time accumulation functions have been modified by the effects of daylength, solar radiation, and sometimes water stress.

Theoretically, if thermal time is accumulated correctly for a given crop variety, then crop development should be directly related to thermal time accumulation, with a characteristic amount of accumulation required for each growth stage or for the appearance of each plant organ (phyllochron) regardless of the time or location of planting. The chapters on phenology models for wheat, maize, sorghum/millet, rice, and cotton show how various modelers have attempted to calculate the accumulation of thermal time, with a considerable degree of success. As can be seen from the leaf and stem development chapters, however, the situation can be quite complicated and is not fully understood.

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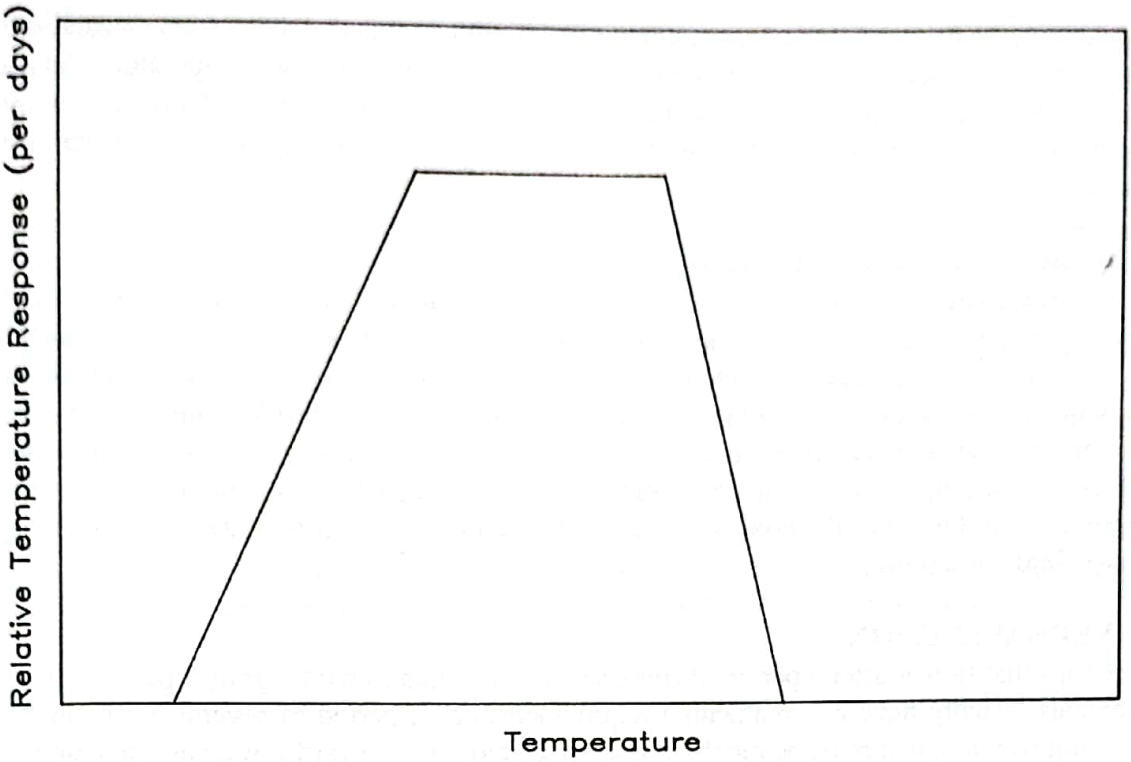

FIGURE 1. Days for the plant to reach some stage as a function of temperature.

1. Simple Thermal Time Equations

Simple thermal time equations or growing degree day (GDD) equations accumulate thermal time linearly with increasing temperature above a constant crop-specific base temperature. There is usually no optimum temperature, although sometimes there is an upper limit above which accumulation is constant. Many such equations have been reviewed by Cross and Zuber,[10] Robertson,[27] Major et al.,[28] and Zur et al.[29] Numerous researchers have expressed reservations about the theoretical validity of simple thermal time equations. Wang[30] noted the base temperature changes throughout the life of the plant. Thornthwaite,[31] Wang,[32] and Padol'skii[33] reported that using various base temperatures or time periods for accumulation did not improve the accuracy of degree day summations as predictors of crop development. Simple thermal time equations ignore thermoperiodicity, the range of temperature between day and night, which has been shown to affect plant response,[34,35] and daylength, which is discussed in a later chapter. In general, these equations are effective only for locally adapted varieties or hybrids over a small geographic range and within a narrow range of planting dates. The equations will have to be rederived for application outside of a limited range of conditions.

2. Photothermal Equations

Photothermal equations are similar to simple thermal time equations, except that daily accumulated thermal time is multiplied by a factor based on daylength. These equations were discussed by Coligado and Brown[36] and by Major et al.[28] Robertson,[27] Williams,[37] and Major et al.[13] developed iterative regression equations combining temperature and daylength effects. Photothermal equations may be usable over a wider range of conditions than simple thermal time equations. However, equations that ignore the negative effects of extremely high temperatures are not suitable for areas with high daytime temperatures during the growing season. They may be used in areas with mild growing season temperatures.

3. Daily Thermal Time Equations

Daily thermal time (DTT) equations accumulate thermal time linearly, with increasing

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temperature up to an optimum temperature or temperature range and thereafter at a decreasing rate with further increases in temperature. Daily maximum and minimum temperatures are used to estimate interpolated temperatures at 3-h intervals throughout the day.[24,26] The rate of daily accumulation is modulated by daylength,[24,26] solar radiation,[25] or daylength and water stress factors.[20]

4. Nonlinear Thermal Time Equations

A set of nonlinear equations have been presented by Kiniry and Keener[12] in which plant development is modeled based on the response of enzymatic reactions to temperature and other factors. Mahan et al.[38] and Burke et al.[39] discuss the reaction rates of several wheat and cotton enzymes over a range of temperatures in terms of crop management and breeding for high yields.

For predicting crop growth stages, the daily thermal time equations have generally been most effective, especially over a range of environments. However, there has been very little experience in the use of the nonlinear, enzymatic-based equations to predict crop phenology under field conditions.

B. VERNALIZATION

Crops that flower after a period of freezing weather, such as winter grains, perennials, and biennials, usually have a vernalization requirement, i.e., a period of several weeks of near freezing weather, that must be met before rapid development toward flowering can begin.[40,41] Without vernalization, flowering of winter grains and some spring grains is delayed.[42-46] Spring grain varieties usually have little or no vernalization requirement,[47,48] although Halloran[49] reported reduced leaf number in response to up to 6 weeks of vernalization for Australian spring wheats. Rahman[50] reported a wide range of vernalization responses for 30 spring and winter wheat varieties.

The vernalization requirement reduces the possibility of floral development beginning during a warm period just before, in the middle, or near the end of the cold season. This is important because plants are least tolerant of cold stress during the time of flowering and the beginning of seed growth. Roberts[51] reported that cold hardiness (ability to survive exposure to subfreezing temperatures) of winter wheat reached a maximum at vernalization and declined shortly thereafter. Winter grain crops, northern temperate perennial fruits,[52] and many biennials have vernalization requirements. Vernalization has been modeled by accumulating vernalization units during near freezing periods and losing accumulated units during warm periods.

Some models have used calender dates to estimate the completion of vernalization for a crop variety, but this will obviously be specific to a location and have no relevance to other varieties or the same variety at a different location or with a substantially different planting date.

The problems to be resolved include determining the minimum, optimum, and maximum temperatures for accumulating and reducing accumulated vernalization units, the growth stage when accumulation should begin, and the rate functions to be used for accumulation. Otter-Nacke et al.[26] (for winter wheat) and Richardson et al.[53] (for peach trees) have developed vernalization models. The vernalization functions for winter wheat are discussed with the CERES-wheat model.

C. HEAT AND COLD STRESS

Heat and cold stress primarily affect plant growth processes, but some phenological processes may also be affected. Major et al.[54] reported delays in panicle emergence and anthesis for sorghum due to chilling.

III. WATER STRESS

The primary effects of water stress are on growth processes (photosynthesis, leaf expansion,

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partitioning). However, several researchers have suggested that mild water stress hastens development while severe water stress slows or stops development in some species.[20,55-58] Stout et al.[59] reported both hastening and slowing of sorghum development by water stress, while Huda et al.[60] reported no change in development rate due to water stress. Multiple regression analysis by Undersander and Christiansen[61] indicated an interaction of water availability with thermal time affecting the time to heading of winter wheat. Yegappan et al.[62] reported reduced leaf number and slower leaf appearance rate, but no change in time of floral initiation for sunflower under water stress. For soybean, Frederick et al.[63] report that water stress starting 2 weeks before flowering had no effect on the flowering date, but delayed the rate at which new nodes appeared. Hodges and French[20] suggest that mild water stress before the beginning of grain growth could hasten development by slightly reducing evapotranspiration and hence increasing plant temperature while severe water stress could disrupt or slow physiological processes by changing osmotic potential or turgor pressure. After the beginning of grain growth, any degree of water stress could hasten senescence of leaves and cause rapid maturation.

Relatively little quantitative information is available on water stress effects on phenology. Attempts to include it in models[20] have not been subjected to quantitative testing.

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Chapter 4

PREDICTING DAYLENGTH EFFECTS ON PHENOLOGICAL PROCESSES

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I. INTRODUCTION

In this chapter we make three points concerning the relationship between daylength and phenological events. The first is that the phenological response to daylength has evolved as a tool to maximize the survival of the species. The second point is that with some notable exceptions, the phenological responses to temperature and daylength are independent. The final point is that the genetic control of the phenological response to daylength controls adaptation, but the seasonal progression toward maturity is mainly determined by temperature. Our general approach in this chapter is to stress similarities of response among species and genotypes within species but confined mainly to crops of agricultural significance. As with all fields of endeavor, there are many ways of investigating the same problem. We hope to illustrate the strengths of the various approaches that are most commonly used. Where possible we demonstrate the similarities in results among the methods and attempt to clarify terminology.

The predominant bias in this chapter, however, lies in our philosophy that the similarities among species and genotypes are more important than the differences. When one considers the vast quantity of literature that is available for the various methods of studying daylength effects on about 50 crop species, it is difficult to visualize a distillation of the theories into a unified model. Biological variability and experimental error further complicate the search for a universal understanding of the problem. This is made even more difficult when we add our own personal and perhaps even cultural biases. By complementing the other chapters in this book we hope to present, to the extent possible, a unified perspective on the daylength response.

II. RESEARCH PHILOSOPHIES IN DAYLENGTH RESEARCH

A. EARLY RESEARCH

General acceptance that daylength controlled phenological events arrived in 1920 when Garner and Allard[1] showed that daylength changed the phenology of soybeans. Much of the research in the next 30 years was conducted at the USDA station in Beltsville, MD.

The multicollinearity of temperature and daylength is probably the factor that has made it so difficult to assign a definite role to daylength. In the temperate regions, daylength and mean air temperature follow a sinusoidal pattern but the maximum temperature occurs about 1 month after the solstice.[2] Added to this complexity is the fact that the natural daylength is always changing. Early daylength studies involved transferring potted plants between a greenhouse and rooms which shortened or extended the daylengths.[3] Another method was to study serial planting dates in a greenhouse in which the annual mean temperature was relatively constant.[4] Throughout the succeeding years there has been a succession of planting date studies with and without temperature control which have enhanced our knowledge of the daylength response.[5]

Simultaneous with the field and greenhouse studies was the search to explain daylength effects at the cellular level. Obviously, a continually changing day/night rhythm has to be explained in terms of circadian rhythms.[6]

In the 1950s phytochrome, the photoreversible pigment located in cell membranes, was discovered. One of the two forms predominates depending on light conditions. This probably controls membrane permeability and also may be responsible for stomatal opening through its control of ATP pumps and the inter-/intracellular potassium balance.[7]

Extrapolation from a circadian rhythm to a sudden change in the apical meristem is difficult but the search continues.[8] This has led to the concept of the flowering hormone, florigen, which has yet to be identified. One current hypothesis is that florigen may simply be a balance of gibberellin and kinetin or some other hormones.[9]

Regardless of how circadian phytochrome rhythms translate into phenological changes, two important points need to be made. The first is that the timing of events is remarkably constant.

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A single genotype seeded on the same date will flower within a few days of the same calendar date every year. The other point is that all higher plants seem to have evolved with daylength responsivity. There are many instances of varietal insensitivity, but there are as yet no examples of an entire species being daylength insensitive. Thus we conclude that daylength insensitivity does not imply a lack of circadian rhythms but simply that the genetic control of the phenological process is not responsive to daylength.

The advent of controlled environment cabinets or growth chambers allowed the separate study of daylength and temperature. However, one difficulty with early growth chamber research was related to inadequate experimental replication. Growth chambers represent a large capital expenditure and are large energy consumers. Consequently, it was not uncommon to use the same growth chamber for an entire experiment or, in daylength/temperature experiments, to have all daylengths for a given temperature in the same growth chamber. Consequently, a 1°C temperature difference between chambers turns out to be a 10% error if the temperature is 20°C and the base for summation of temperatures is 10°C. Another error is that there are usually three or more mechanical clocks, typically with 5 to 15 min gradations, controlling the lighting in a growth chamber. These clocks are subject to losing or gaining about 0.5 h every 50 d, so it is possible that the daylength might be 1 h longer at the end of the experiment than it was at the beginning. New electronic controls have resolved this problem, but the temperature bias still has to be eliminated through accurate calibration and appropriate replication.

In spite of these problems, growth chamber studies have been the key to increasing our knowledge of the daylength response. It was in growth chamber manipulations of the day/night rhythm beyond 24 h that we found that the length of the night rather than the daylength actually controls the phenological response in short-day plants. However, since in nature the 24 h rhythm prevails, so too do the terms daylength and photoperiod.

B. ABSOLUTE VS. QUANTITATIVE DESCRIPTORS

Garner and Allard[10] realized that annual crop species fall into two categories, long-day plants or short-day plants. A short-day plant completes its development in less time in short daylengths, and a long-day plant takes less time in long daylengths. The response is not linear, however, and as a result there have been various designations for the various types of responses.

One approach, which we have chosen to call absolute, separates cultivars or species according to whether they are obligate or facultative. In fact, Salisbury[11] developed a scheme in which examples are given for 777 classifications ranging from a simple description such as "day-neutral, no causative temperature effect" to more complicated descriptions such as "long-day plants; no causative effect of temperature; critical dark period inversely proportional to temperature". Unfortunately, using this scheme, genotypes of a given species fall into many different categories and the information is of limited value in computer modeling of the daylength response.

Although some controversy may still exist, it is likely that the temperate cereal grains — wheat, barley, oat, and rye — are all long-day species,[12,13] and maize, sorghum, rice, and soybeans are short-day species.[12,14-16]

In the quantitative approach, an attempt is made to express the daylength response in terms of parameters of a mathematical model. There are many methods of doing this, some combining temperature and photoperiod,[17,18] and one that even includes a term for water stress.[19] In general, two methods are used to relate development to photoperiod when all other environmental factors are held constant, and they are discussed in detail in Sections III.B and III.C of this chapter. The difference in these two methods is that one relates the duration between events to daylength and the other relates rate of development, calculated by inverting the duration, to daylength. The value of the quantitative response approach is that the model parameters can be used in computer models to predict the date of phenological events.

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C. TIME INTERVAL BETWEEN EVENTS VS. DURATION OF EVENTS

The scope of daylength response studies is based either on prediction of the date of an event, such as anthesis, or on the duration of an event, such as the reproductive phase and the amount of leaves or florets that are initiated during the interval.

The simpler of the two is to model the onset of the phenological event. Theoretical models based on growth chamber data[20] or empirical models usually based on field data[21,22] have been used. When these development models are coupled with yield or photosynthesis models they have tremendous value for monitoring condition and yields of important crops. Input for the development portion of the model usually requires only air temperature and daylength and an estimate of seeding date.

Depending on the model, a genetic component for the daylength parameters also might be included. A refinement of the models described is to relate daylength to plastochron or phyllochron so that the leaf number and position are also known at the time of the phenological event. The plastochron is the time interval between periodic events and in crop development the periodic event usually has been assumed to be the initiation of new leaf primordia.[23] The term phyllochron refers to the time interval between the appearance of new leaves and was coined to differentiate the two.[24] The reason for differentiating the two terms is that the appearance of a leaf tip is not the same as the initiation of new primordia. After the first flower is initiated, the total number of florets initiated or the duration of flower initiation is also influenced by daylength.

III. PHENOLOGY AS AN EVOLUTIONARY PROCESS

A. MAXIMIZING SEED PRODUCTION THROUGH FLOWERING DATE

Daylength provides plants with a consistent environmental variable for controlling date of flowering. At a given latitude, photoperiodism ensures that plants will flower near the same day of year every year. It is not surprising that daylength-controlled mechanisms have evolved for maximizing seed production and quality to aid survival of plant species. Such consistency in flowering date is important in temperate regions and tropical regions for two different survival strategies. In a temperate climate, seed production must be completed before immature embryos or seeds are killed by autumn frosts. Conversely, premature senescence results in low seed production and also may result in deterioration of seed exposed to long periods of warm moist conditions. Thus, species have survived which optimize their seed production depending on when they emerged as seedlings.

Planting date studies demonstrate this optimization of flowering date very well. Plantings at various dates will often flower on the same or nearly the same date.[25] While low temperatures during early development contribute to the delay in flowering for early plantings in temperate regions, photoperiodism is also important. Floral initiation of long-day plants is delayed until the daylength is sufficiently long.[26]

In order to understand the importance of the sensitivity of short-day plants to daylength, one must look at their regions of origin. Sorghum and maize, both short-day plants, are of tropical origin. Their sensitivity is important for inducing flowering during the most productive season relative to rain, as discussed previously. Breeding programs for producing maize and sorghum cultivars for temperate regions have included reduction or elimination of photoperiod sensitivity. In more northern environments, reduced photoperiod sensitivity, along with reduction of the basic vegetative phase, has provided hybrids that mature in very short growing seasons. Thus, one concludes that daylength effects play an important role in determining the region of adaptation.[27] However, during the growth cycle, daylength effects are less important than temperature effects.

B. PHASES OF DEVELOPMENT

Many phases have been devised to describe crop species in terms of their progression toward

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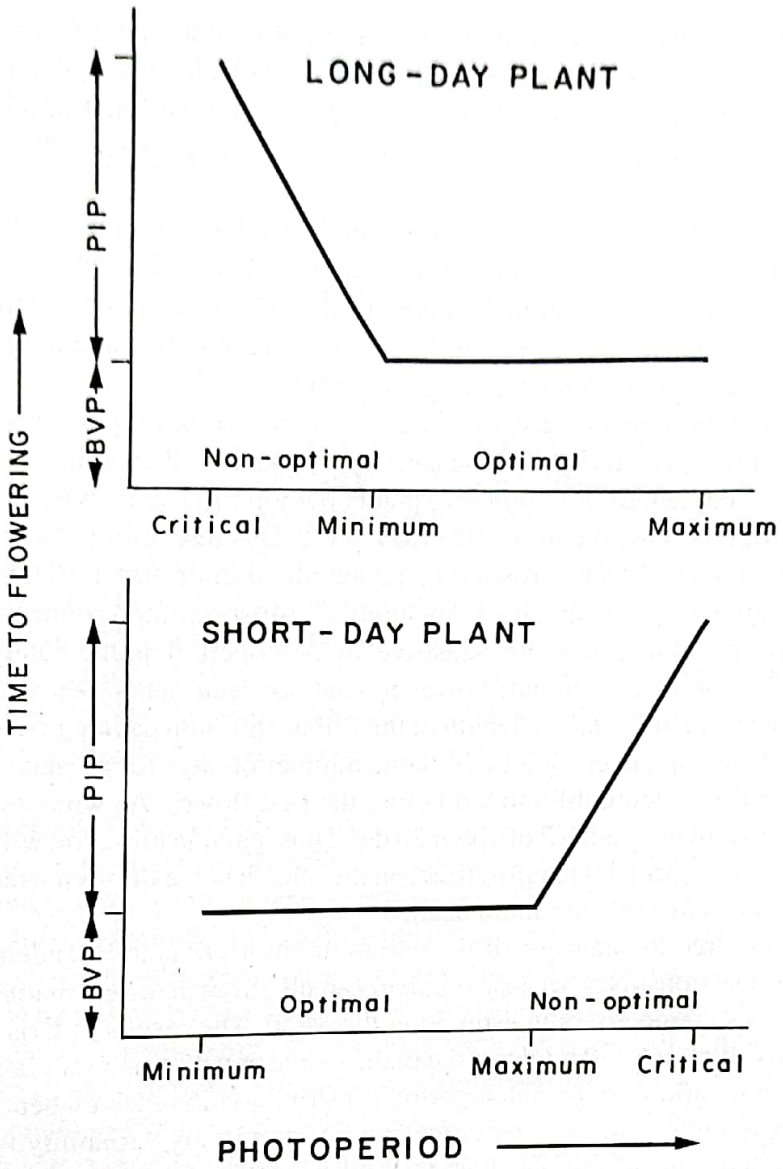

FIGURE 1. Responses of long- and short-day plants to photoperiod. PIP = photoperiod-induced phase; BVP = basic vegetative phase.

maturity. They generally fall into the qualitative and quantitative types. The sorghum and rice examples are ideal because (1) the number of phases is only three, (2) the transition to each phase is marked by an easily identifiable stage,[28,29] and (3) each phase is identifiable regardless of environmental conditions. The phases include the vegetative phase ending with panicle initiation, the reproductive phase ending with anthesis, and the ripening phase ending at maturity.[30] The disadvantage of these phase designations is that they do not provide any information with respect to plant size or leaf number as do the wheat, maize, rape, sorghum, or soybean growth stage schemes.[31-35] These types of staging scales become complicated when used to describe a range of cultivars because of variability in total leaf numbers.

C. ANALYSIS OF DAYS OR THERMAL TIME VS. DAYLENGTH

Daylength effects are most often apparent on the length of the vegetative phase. In this chapter most of the discussion is directed to this phase.

Major[20] developed a system of describing daylength responses that is universally applicable, is amenable to genotypic and species differences, and provides useful criteria for computer modelers (Figure 1). While originally developed for rice by Vergara and Chang[30] the system has been applied to a wide range of crop species, with modifications in terminology. In this system

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the vegetative phase is broken down into a juvenile phase and a photoperiod-induced phase (PIP). The juvenile phase is independent of daylength but can be of variable length depending on genetic control. The minimum duration from seedling emergence to floral initiation, termed the basic vegetative phase (BVP), is the sum of the juvenile phase and the PIP in optimum daylengths.

The length of the PIP is controlled by daylength. Under optimum daylength conditions duration of the PIP is a constant, minimal number of days. Nonoptimal daylengths increase the length of the PIP. The maximum optimal photoperiod for short-day plants, or minimum optimal photoperiod for long-day plants, is the threshold between optimal and nonoptimal daylengths. These thresholds are, for convenience, designated MOP.

Nonoptimal photoperiods increase the duration of the PIP in proportion to the genetically controlled photoperiod sensitivity. This sensitivity can be described in units of days delay per hour of increase in daylength. For long-day plants photoperiod sensitivity is negative. Maize plants are only directly sensitive to photoperiod in the days just prior to tassel initiation. This interval is 4 to 5 d long for plants growing in daylengths shorter than 12.5 h but is longer with photoperiod-sensitive cultivars in longer daylengths.[36] Most common soybean cultivars apparently lack a juvenile phase and are sensitive to photoperiod immediately after seedling emergence. Wilkerson et al.[37] found, however, that soybean genotypes which have a long juvenile phase can be identified. The length of the PIP in optimum daylengths is constant across genotypes, with flowering occurring in the same number of days for all genotypes under such conditions.[37] The PIP lasted until 6 to 9 d before the first flower. As with soybeans, sorghum cultivars apparently all have a BVP of about 20 d.[28] Thus, panicle initiation will occur 20 d after seedling emergence in short daylengths. Rice, on the other hand, exhibits a wide range of values of the BVP,[30] as does maize[38] and mungbean.[39]

Research is required to determine if the variability in MOP is independent of photoperiod sensitivity. This question arises because relatively small errors in the estimation of photoperiod sensitivity can cause large errors in estimating the MOP. The results of Criswell and Hume[40] suggest that variability in MOP might be the main source of variation in soybean photoperiodic response, although variability for photoperiod sensitivity is indicated when a wider range of maturity is considered.[27,41] Most other crops exhibit little if any variability for this character. MOP was not included in the original photoperiod description of Vergara and Chang so one must interpret their graphic presentations of rice results. From the data presented in the Appendix of the bulletin prepared by Vergara and Chang,[30] it is reasonable to assume that rice cultivars have MOPs that vary from less than 10 to more than 13 h. The MOP is consistently 12.5 h for maize[38,42] and 12±1 h for sorghum of several maturity types.[43] Mungbeans have an MOP that varies from 12 to more than 14 h.[44] The mean MOP for a number of long-day crops, including wheat, barley, oat, rye, flax, and rape, is 17.7 h and appeared to not vary among species or cultivars.[20] The MOP for 10 oilseed rape cultivars also did not vary and the mean value was 17.1 h.[45]

Photoperiod sensitivity expressed as days delay of flowering or floral initiation per hour increase of daylength almost always varies among cultivars within a species. In rice it varies from 0 for cultivar Tainan 3[30] to about 200 d/h for cultivars such as Skrivimankoti.[46] Maize photoperiod sensitivity varies from 0 to more than 2 d/h[36,47] or from 0 to 2 leaves/hour.[38] In an analysis of Garner and Allard's[10] data, Major[26] found that photoperiod sensitivity varied from 2.5 d/h for "Mandarin" soybeans to 147 d/h for "Biloxi". Byth,[48] Cregan and Hartwig,[27] and Jones et al.[41] found differences in soybean photoperiod sensitivity. Sorghum photoperiod sensitivity apparently varies from 0 for the lines containing the Ma_3 allele from Ryer[43] to over 40.5 d/h.[49] In long-day species, the only reported differences are between the conventional northern wheats (–15 d/h) and the semidwarf, the latter being less sensitive (–5 d/h).[20] King and Kondra[45] found no differences among rape cultivars with a mean of about –2.7 d/h. Major[20] found a mean value for 4 rape cultivars of –6.8 d/h. The range of values used in the CERES-wheat model is –100 to –500 GDD_0, which would translate to –4 to –20 d/h at 25°C.

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In the originally proposed model there sometimes appeared to be a critical daylength which defined either the beginning of a response plateau for extreme nonoptimum daylengths or the most extreme nonoptimum daylength at which flowering will occur. Thus, when the daylength is longer than the critical photoperiod for short-day plants or shorter than the critical photoperiod for long-day plants, floral initiation occurs in the same number of days regardless of daylength, or it never occurs. This implies that there is a basic rate of development even if daylength is longer than the critical photoperiod for short-day plants. This has been occasionally observed for soybeans[48,50] and for maize.[47] Roberts et al.[18] describe this as the "ceiling photoperiod".

D. ANALYSIS OF RATE OF DEVELOPMENT VS. DAYLENGTH

While the daylength response often has been expressed with duration of an interval as a segmented function of photoperiod, there is evidence that rate of development as a function of photoperiod may be more appropriate. Rate, or inverse of duration, is more consistent with enzyme kinetics[51] and basic plant physiology. However, while rate may be more appealing mechanistically, from an applications viewpoint either approach is adequate. One argument for using rate is that the apparent nonlinear or segmented response function with duration becomes linear when rate is used.[52] A similar situation exists with duration of grain-filling of cereals as a function of temperature.[53,54] However, even rate of development can show a segmented or nonlinear response to photoperiod in some cases.[18] In addition, variability in measured data is often too great to justify choosing one approach over another.

E. THE REPRODUCTIVE PHASE

In this chapter, we use the term "reproductive phase" as originally proposed by Vergara and Chang,[30] although it may be more aptly referred to as the preanthesis phase. The daylength response of the interval from floral initiation to anthesis appears to differ among species. It is important to differentiate direct sensitivity to daylength during this interval from the secondary response of anthesis delays due to increased number of leaf primordia initiated when floral initiation is delayed by nonoptimum daylengths. Maize provides an example in which long daylengths increase the duration of the reproductive phase without the plants being directly sensitive to daylength in this interval. Each unit delay in floral initiation results in a 1.2 to 1.4 unit increase in the interval from floral initiation to anthesis.[42,55-57] However, daylength switching treatments indicate that, for maize, direct sensitivity to daylength ends at tassel initiation.[36] Thus, the delay in tassel emergence appears to be due to an increased number of initiated leaves. This lack of daylength sensitivity following floral initiation does not appear to be general among crop species, however. Panicle emergence of rice can be prevented by long daylengths after floral initiation,[58,59] and the reproductive primordia can revert to vegetative primordia if photoinduction is incomplete.[60]

Likewise, the increase in the interval between floral initiation and anthesis of wheat, barley, and oats observed in noninductive daylengths[61-64] also may be a direct response to daylength. Spike emergence of barley has an absolute long daylength requirement even though spike initiation does not.[13] Unfavorable daylength conditions can result in development of abnormal floral structures in wheat.[65] Long daylengths after floral initiation of Biloxi soybeans can delay development of flower buds.[37,66]

In spite of the daylength sensitivity after floral initiation in some crops, the most critical sensitivity for cereal crops is during the interval from seedling emergence to floral initiation. Duration of this interval determines total number of leaves initiated and thus the number which must emerge prior to flower appearance. In addition, winter annual cereals reach floral initiation in periods of increasing daylength. Thus short, noninductive daylengths will not occur between floral initiation and anthesis. Spring-sown short-day crops in temperate regions could experience longer, less optimum daylengths in the period between floral initiation and anthesis than prior to floral initiation.

With this in mind, daylength sensitivity for some crop species, particularly cereals, need only

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be considered when predicting date of floral initiation. Delays in floral initiation due to maturity type or nonoptimum daylengths can then be related directly to duration of the interval ending at anthesis. For example, Kiniry et al.[36] found a good relationship between growing degree days (GDD) from emergence to tassel initiation of maize and GDD from emergence to anthesis. There was an intercept of –25.9 and a slope of 0.46. GDD in this chapter are defined as the mean of the maximum and minimum temperatures minus a base temperature with the condition that if either temperature is less than the base it is set equal to the base temperature. Unless indicated by a subscript, the base temperature is 10°C. Others55-5[7] plotted leaf numbers at tassel initiation on the abscissa and final leaf numbers on the ordinate for various daylengths and temperatures and obtained a good relationship with a slope of 0.42 to 0.44 and intercept ranging from –1.95 to –2.30 leaves. The remarkably similar slopes from these independent studies are also similar to the ratio of 0.54 for GDD_8 per leaf primordia divided by GDD_8 per leaf tip found by Kiniry and Ritchie.[67] In addition, the negative intercepts of these relationships can be accounted for by the six-leaf primordia present in the maize seedling at emergence.[67,68] These results suggest that the longer the interval from emergence to tassel initiation, the longer the interval from tassel initiation to anthesis.

A relationship also exists for sorghum based on data from Quinby and Karper[69] and Castleberry[70] in which the slope is 1.01 GDD_8(em-pi)/GDD_8(em-an) and the intercept is 626 GDD_8(em-an). This differs from maize, however, in that a constant 626 GDD_8 are required from panicle initiation to anthesis.

The slope of the relationship for rice, based on combined data of Sircar and Sen,[71] Velasco and Manuel,[72] Tang and Liu,[73] Sen and Roy,[74] and Misra and Khan,[75] is 1.37 d (from sowing to panicle emergence) per day (from sowing to panicle initiation) with an intercept of almost 0.

The comparable relationship for wheat from Riddell et al.[76] has a slope of 1.97 GDD_0 from emergence to floral initiation per GDD_0 from emergence to anthesis.

These relationships are useful and valuable in computer modeling of crops and in the interpretation of data from various types of studies.

Thus, in most cereal crops, the reproductive phase is related to the time between seedling emergence and floral initiation. Consequently, the time from emergence to anthesis is proportional to the time from emergence to floral initiation or terminal spikelet. However, the time from anthesis to physiological maturity fails to show a strong relationship to duration of earlier phases.

F. THE MATURATION PHASE

The period between flowering and maturing was called the maturation phase by Vergara and Chang.[30] The growth habit plays a critical role in the environmental response of the duration of the maturation phase.[77] Indeterminate species such as soybeans or cotton produce flowers over a long period of time if the environment is favorable. Graminae crop species show differences of only a few days in dates of maturity of florets within the inflorescence.

While the period from sowing to anthesis has been shown to be correlated sometimes with the duration from anthesis to maturity for different maize cultivars,[78,79] there are differences in duration from the anthesis to maturity among cultivars of the same maturity.[78-81] In addition, there is no evidence that photoperiodic delays in the reproductive phase alter the duration of the maturation phase.

This interval for wheat and barley is probably also independent of daylength, although Guitard[61] reported a decreased number of days from heading to maturity for barley when daylength increased in growth chambers, and an iterative regression procedure using field data of wheat indicated a daylength response for the interval.[21] However, Marcellos and Single[2] found that the development rate after flowering of wheat was independent of daylength.

Soybean represents an indeterminate species for which maturity can be delayed by long daylengths. Using Robertson's[21] iterative regression technique, Major et al.[22] found that the

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anthesis to maturity interval was related to daylength. Other studies[25,41,82,84] also indicated that long daylengths can delay postflowering development of soybean. Even some cultivars that are insensitive to daylength in preflowering stages can have delayed maturity in long daylengths.[85]

IV. INTERACTION OF DAYLENGTH AND TEMPERATURE

Identification of interactions between daylength response and temperature response in the field are difficult because of the seasonal trends of both environmental variables. As daylength increases in the spring, temperature also increases. Simple descriptions of daylength responses in terms of days have led to numerous reports of such interactions. Low night temperatures hasten flowering of rice in short days but not in long days.[86] Temperature during the night was more important for soybean development than temperature during the day.[3,87] Similarly, shorter daylengths were required for flowering of soybeans with cooler night temperatures.[88] A single maturity gene of sorghum (Ma_2) has even been identified as apparently mediating a temperature × daylength interaction.[43]

It has been suggested that decreased daylength sensitivity leads to increased thermosensitivity. Rice cultivars that were least sensitive to daylength have been reported to be the most sensitive to temperature.[89,90] However, the results of Vergara et al.[91] indicated that the most daylength-sensitive rice cultivars were also the most sensitive to temperature. Similarly, Kuriyama,[92] studying rice cultivars of diverse origin, concluded that cultivar differences existed for both daylength and temperature sensitivity but that there was no relationship between daylength response or temperature response. Temperature effects on field-grown soybeans have been reported to be apparent only when daylengths were short and temperatures were cool.[5]

The description of daylength sensitivity in units of thermal time may eliminate much of the temperature × daylength interaction evident when units are days. There is increasing evidence that plant responses to daylength and temperature are independent when each is adequately described.[50,84] Kuriyama[92] failed to detect any effect of temperature on the optimum daylengths or daylength sensitivity of rice.

Application of a thermal-time system requires accurate expression of the development rate response to temperature. The commonly used GDD represents a crude approximation of a complex biological response. Each error in estimation of thermal time is cumulative and can easily exceed 10%. For this reason, the choice of the thermal-time scale for expressing duration or rate of development as a function of daylength is important.

A. SCALES USED FOR DAYLENGTH RESPONSE

Three scales can be used to measure phenological time: calendar days, thermal time, and leaf number. These vary in complexity and in dependence on temperature. There are advantages and disadvantages to each scale.

Calendar days represent the oldest and most easily applied system. Obviously, temperature differences will alter the magnitude of the daylength response parameters. This scale is most useful for describing results when the temperature is held constant.

The thermal-time or physiological-day scale is designed to quantify development rate responses to temperature. The physiological day is obtained by dividing the thermal unit accumulation by a value representative of a day when temperature is optimum all day. To be completely independent of temperature, the function must exactly duplicate the thermal response. The temperature response may vary among genotypes and among stages of development. This scale is widely used, particularly for field experiments with variable temperatures.

The leaf number scale is feasible for determinate species because leaves on the main stem are initiated at a temperature-dependent rate. Final leaf number is sometimes influenced by temperature, but this effect is slight. The practical problem with leaf number is accounting for lower leaves that are lost prior to flowering. Steps must be taken to account for such leaves.

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B. EXTREME INTERACTIONS

Using the thermal-time scale or leaf numbers generally demonstrates that the temperature and daylength responses are independent. However, extreme values for either environmental variable may result in dramatic interactions.

Historically, vernalization has been a common candidate for such temperature × daylength interactions. In wheat, vernalization was reported to reduce the requirement for long days.[93-95] The effect of cold temperature has been reported to be more effective in inducing barley flowering when accompanied by short daylengths.[18] Such interaction between vernalization and daylength responses is not universally accepted, however.

Two independent sets of genes control the vernalization and daylength responses.[96-98] In addition, other researchers have found that vernalization does not reduce the daylength sensitivity.[99-103] It appears that vernalization alters the duration of the juvenile phase and daylength acts independently on the succeeding PIP. Sorghum and maize development in the tropics represents additional cases of daylength × temperature interactions. Short winter daylengths at tropical locations result in delays in panicle emergence of sorghum[49] and silking of maize.[104]

Milo lines have more leaves at 30°C than at 25 or 20°C in nonoptimal daylengths.[43] It may be that these interactions are due to deficiencies in photosynthate availability caused by short days, with insufficient quantities of solar radiation to meet the energy requirements of the plant.

V. EFFECT OF DAYLENGTH RESPONSE ON ADAPTATION

A. EFFECT OF LATITUDE

While daylength varies consistently with latitude, large scale climatic differences alter the seasonal temperature profile at different longitudes. Thus, genotypes are not adapted to all longitudes. Surveys of genotypes and their region of adaptation suggest that the effect of a decreasing latitude is that genetically adapted plants tend to have a longer juvenile phase and decreased daylength sensitivity. For an adapted short-day plant, the juvenile phase also increases as the latitude decreases but the daylength sensitivity increases.

As latitude decreases, the adapted long-day plant changes from spring to winter habit and it is grown in shorter and shorter daylengths. The onset of rapid growth is controlled by temperature.[105] Thus, the southern-adapted cereal such as Pitic wheat has a lower daylength sensitivity than the northern cultivar such as Thatcher or Park[20,106] but, in the southern latitudes, it is affected more by daylength because it is growing in winter during nonoptimal daylengths. Thus, a Canadian wheat takes longer to mature in a winter nursery in California than a California cultivar, but the Canadian wheat is earlier when it is grown as a spring cereal in Canada.

B. EFFECT OF PLANTING DATE

For most short-day plants, adapted genotypes exhibit a 1-d delay in flowering for every 2 d delay in planting. The effect is similar for spring-seeded long-day plants in cool temperate climates. For winter-habitat long-day plants, the effects are somewhat more muted, depending on the severity of winter.

Major[26] applied the basic flowering model to 9 species of greenhouse-grown plants seeded fortnightly at 49° latitude. The model works for both short- and long-day plants and so provides an idea of how daylength influences development in the field. Since temperatures usually peak 1 month after the solstice, short-day plants are likely affected to some degree by the long daylength, regardless of seeding date. Late-seeded short-day plants, such as soybeans planted after winter wheat, will be exposed to warm temperatures and rapidly decreasing daylengths.

Short-day plants seeded in late April and May are subjected to lower spring temperatures and nonoptimum daylengths so that flower initiation is delayed by cool temperatures and long daylengths. In spring, the winter annual long-day plants are delayed by cool temperatures and

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short daylengths, but as summer approaches, the increasing temperatures and daylengths work together to hasten development.

C. GENETIC VARIABILITY OF DAYLENGTH RESPONSES

In the past decade, a picture of the type of variability that exists for the daylength responses has emerged. Rice has been the most extensively studied in this respect and, not surprisingly, shows variability for BVP, MOP, and daylength sensitivity. Studies of North American cultivars have revealed lower variability. A study by Criswell and Hume[40] suggested that in early maturing soybeans, the only variability was in the MOP, with BVP and daylength sensitivity essentially the same for all U.S. cultivars. In sorghum the BVP and MOP appear to be constant, with daylength sensitivity changing and additional variability coming from temperature sensitivity. Maize seems to have a constant MOP but the BVP varies among maturity types. Wheat appears to be relatively constant in terms of MOP but varies in BVP and daylength sensitivity. There is also variability for vernalization.

Some studies suggest that inheritance of the BVP is dominant in wheat and maize and that daylength sensitivity is also dominant. This gives rise to the interesting situation in which lateness and earliness are both dominant characteristics and helps explain how relatively few genes can control a seemingly complex response. Control of the MOP may or may not be linked to daylength sensitivity. Correlations between the MOP and daylength sensitivity generally suggest that they are associated, but it should be remembered that this could be an artifact if the same regression technique was used to calculate both parameters.

VI. CONCLUSIONS

There is agreement in principle on the response characteristics of a wide range of crop plants. Whether expressed as time or as the inverse of time (rate), there appears to be a juvenile phase, which is independent of daylength, and a daylength-sensitive phase, which controls the initiation of the reproductive structures. There is an increased awareness of the effects of temperature on phenology, but a feeling that actual temperature-daylength interactions exist but are modifiers of the response. There is also a general acceptance that we need to catalog the genetic differences for the various phases. A benefit of crop modeling has been the encouragement of mathematically based phenology models, resulting in more quantitative descriptors and providing indirect proof that the growth chamber-based models are realistic. Perhaps, most importantly, there is a growing consensus among scientists that daylength research is moving in the right direction.

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Chapter 5

PREDICTING LEAF DEVELOPMENT OF CROP PLANTS

J. R. Kiniry, W. D. Rosenthal, B. S. Jackson, and G. Hoogenboom

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I. INTRODUCTION

Leaf development is strongly interrelated with phenology in a number of ways. The total number of leaves of a given shoot (and often of the entire plant) is related to the duration of the development interval to floral initiation, as well as to the rate of leaf primordia initiation. The total number of leaves and rate of appearance directly relate to the development of the plant toward anthesis. Once final leaf number is determined, these leaves emerge before the flower becomes visible and anthesis occurs. In some conditions, such as in cases of drought stress with maize, the anthers actually dehisce prior to emergence of the male flower. However, these situations are rare.

Efforts to simulate leaf area in relation to phenology have resulted in models of varying complexity. In its simplest form, potential leaf area per plant or leaf area index (LAI) is modeled as a direct function of total number of leaves or duration of the period of vegetative growth.[1,2] A more complex modeling approach in common use involves modeling areas of individual leaves.[3-6] In this approach, leaf initiation, leaf tip appearance, leaf expansion, and leaf senescence are all simulated. Finally, some models are intermediate in complexity between these two.[7] Such models may describe leaf initiation and tip appearance in an effort to predict total number of leaves and date of anthesis. In such cases, leaf area development may be simulated only on a whole-plant basis.

Leaf development is visible and easily measured prior to anthesis. Thus, it is easy to understand the attractiveness of this subject for researchers interested in vegetative stage development. Aitken[8] discussed both the interval between initiation of formation of successive leaf primordia (plastochron) and the interval between the opening of two successive leaves (phyllochron) for wheat, barley, oat, and rye. For the following discussion, phyllochron refers to the interval between appearance of successive leaf tips or trifoliolate tips outside of the leaf whorl, rather than to the opening of leaves. This definition is essentially identical to the other for plants with only one leaf expanding at a time. However, for species such as maize, in which as many as four not-fully-expanded leaf tips may be outside the leaf whorl at one time, the definition using leaf tip appearance is more useful. The degree days (base 8°C) between emergence of successive leaf tips of maize is fairly constant on a plant after the second leaf. However, differences in the duration of the tip emergence and the collaring interval among leaves on a plant cause the degree days between appearance of leaf ligules to vary greatly.

In this chapter we investigate the three major processes involved in leaf development which relate to phenology: (1) leaf primordia initiation, (2) leaf tip appearance, and (3) leaf expansion. Values for the base temperature for each development rate, the cumulative degree days required per leaf event, and the effects of stress and cultivar on the rate will be discussed for various crop species.

A. IDEAL LEAF DEVELOPMENT SCHEME

When modeling complex systems such as the development of leaves, it is often valuable to develop a simple system, derive constants for the crop species of interest, and test on field data before more complex approaches are attempted. Growing degree days (GDD) calculation represents one such approach. For this chapter, GDD_{tb} for 1 d are calculated with the same form as the "heat stress" equations of Gilmore and Rogers,[9] with development rate increasing linearly above a base temperature (t_b in Figure 1) up to an optimum temperature (t_{opt}) and thereafter decreasing linearly to zero rate at a maximum temperature (t_{max}).

In addition to simplicity of derivation and application, there are three other reasons why this form could be preferable to the nonlinear systems often described. First, development rates which have been used to derive nonlinear equations are often based on either split day/night temperature data or temperatures too low for long-term plant viability. A split day/night temperature treatment should have a development rate similar to the rate in a constant temperature treatment with the same mean only if the day and night temperatures both are

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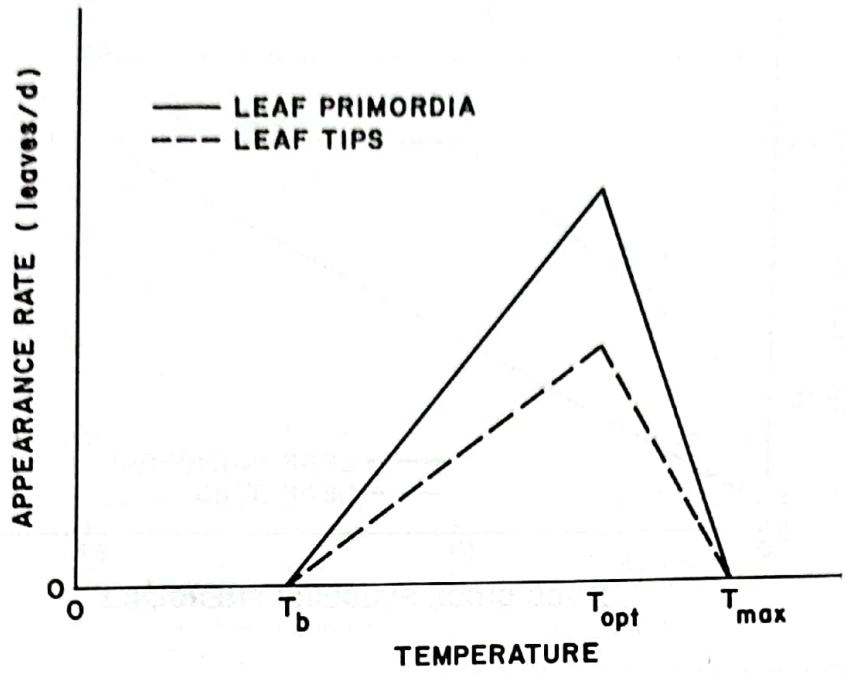

FIGURE 1. Idealized leaf development rate response to temperature. The three cardinal temperature variables are base temperature (t_b), optimal temperature (t_{opt}), and maximum temperature (t_{max}).

between t_b and t_{opt} or both are between t_{opt} and t_{max}. If the day temperature is greater than t_{opt} and the night temperature less than t_{opt}, the rate of development should be less than for the constant temperature treatment with the same mean temperature, thus making the rate appear curvilinear when actually a two-step approach as described here may be more appropriate. From an application standpoint, when daily maximum or minimum temperature falls outside the t_b to t_{opt} range, sine wave interpolations similar to those of Fry,[10] as described in Jones and Kiniry,[7] can be used to compute several rates for a day and the mean rate thus calculated.

A second justification for use of this GDD system is that errors in predicting development rate at temperatures near t_b are often negligible when predicting development with field data. Development rate predictions are at their lowest near t_b and such GDD values comprise only a small percentage of the total.

Finally, attempts at prediction in the field using curvilinear equations for rate as a function of temperature have failed to prove superior to GDD equations and in many cases have been inferior. Prediction of development stages of maize was attempted with a curvilinear equation,[9,11] and such systems proved to be less accurate than GDD equations.

Thus, for this chapter, the "heat stress" GDD system will be used to describe leaf development. This does not preclude future application of nonlinear temperature response functions, but it does suggest that such approaches be examined very critically before they are accepted.

The relationship between the interval between initiation of leaf primordia (plastochron interval) and the phyllochron interval, both in degree days, is closely related to the relationship between the seedling emergence to floral initiation interval and the seedling emergence to anthesis interval, again both in degree days (Figure 2). Delays in floral initiation, whether due to maturity genotype or photoperiod, allow formation of additional leaf primordia, thus providing additional leaf tips which must emerge prior to anthesis.

Degree days, with a decrease in rate of accumulation when temperatures exceed the optimum, provide a useful means of describing both plastochron and phyllochron intervals. Both rates of leaf primordia initiation and leaf tip appearance increase with increased temperature above a base temperature, up to an optimum. For maize, analysis of data for both plastochron[12] and phyllochron[13] indicated the base temperature is 8°C and the optimum 34°C.[14]

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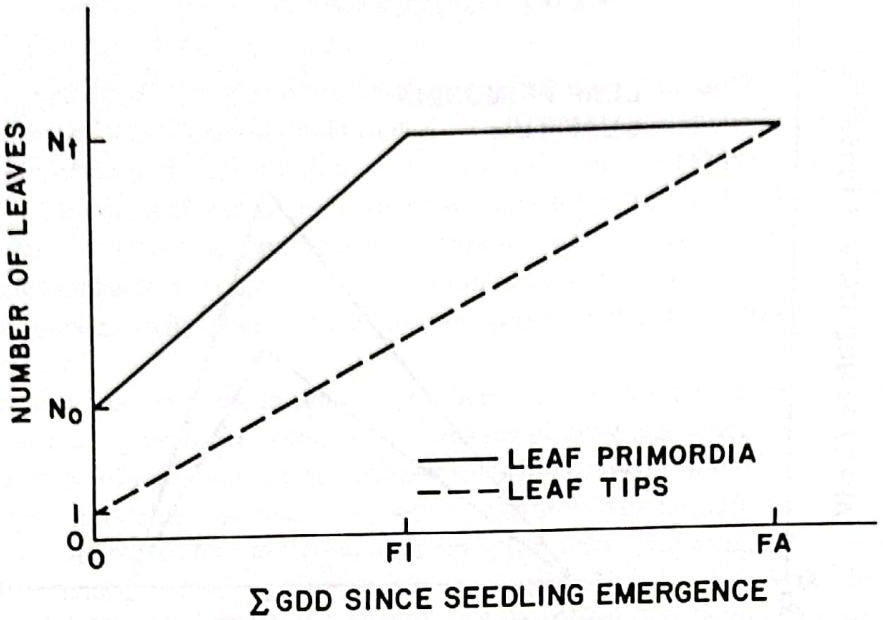

FIGURE 2. Idealized scheme for leaf development. Leaf primordia initiation begins at seedling emergence with a species-specific number of primordia (N_o) already present and stops at floral initiation (FI) at which time the total number of leaves (N_{total}) have been initiated. Leaf tip appearance begins with one at seedling emergence and concludes at anthesis (FA).

GDD sums to predict the number of leaf primordia initiated or the number of leaf tips emerged are also needed for this leaf development system. Assuming the parameters of t_b, t_{opt}, and t_{max} are correct, the simplest scheme would be a given GDD sum required for initiation of each primordium and appearance of each leaf tip. This assumes the leaf development rates are independent of leaf position, as has been shown to be true for maize.[14] The number of leaf primordia present at seedling emergence (N_o) can be determined by linear extrapolation of counts back to summed GDD = 0, as was done by Warrington and Kanemasu.[12] The summed GDD at floral initiation (FI) can be a function of cultivar, photoperiod, and, for winter cereals, vernalization. Total number of leaves (N_{total}) is easily calculated by:

$$N_{total} = FI/Plastochron + N_o \quad (1)$$

The total GDD from seedling emergence to flower appearance (FA) is calculated by

$$FA = (N_{total} - 1) * Phyllochron \quad (2)$$

More rapid appearance of the first two or three leaves can cause an error which should be corrected with some plant species. However, for the purposes of this chapter such effects will be ignored.

With this system, the interaction of leaf development with phenology can be described without involving duration of expansion of individual leaves. However, determination of duration of expansion is valuable when modeling leaf area. As is seen with maize,[14] duration of expansion is more complex than tip appearance or primordia initiation, as it varies with leaf position. Leaf duration of expansion is strongly correlated to final areas of each leaf, as the largest leaves on a maize plant require the greatest time to expand. For simplicity, the GDD system described previously will be used for duration, with the GDD required being a function of leaf position.

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TABLE 1
Sources of Data and Functions for Leaf Development

Plant species	Ref.
Maize (*Zea mays* L.)	14,66,67
Sorghum (*Sorghum bicolor* L. Moench)	3,68,69
Pearl millet (*Pennisetum typhoides* S. & H.)	69,70
Wheat (*Triticum aestivum* L.)	24,31,58,71-73
Barley (*Hordeum vulgare* L.)	44,73
Rice (*Oryza sativa* L.)	69,74,75
Cotton (*Gossypium hirsutum* L.)	65,76-80
Soybean (*Glycine max* (L.) Merrill)	48,81-85
Sunflower (*Helianthus annus* L.)	45,86-88
Cowpeas (*Vigna unguiculata*)	89
English peas (*Pisum sativum* L.)	8,86
Faba bean (*Vicia faba* Maris Bead)	46
Sugarbeet (*Beta vulgaris* L.)	90-92
Subterranean clover (*Tricolium subterraneum* L.)	8
Velvet leaf (*Abutilon theophrasti*),Lambsquarter (*Chenopodium album* agg.), Pigweed (*Amaranthus hybridis*), and Cocklebur (*Xanthium canadense*)	86
Cocklebur (*Xanthium pennsylvanicum* Wallr.)	93
Banana (*Musa* sp.)	55

II. RESULTS

A. LEAF APPEARANCE RATE

Due to the scarcity of data (Table 1) related to leaf initiation rates, only comparisons of leaf appearance rates will be made in the following discussion. However, the initiation rate data are provided for future reference (Table 2).

The results for base temperature for the major warm-season grain and oil crops are strikingly similar (Table 2). It appears that a base temperature of 7 to 9°C could be used for maize, sorghum, pearl millet, rice, soybean, and sunflower. The greatest differences among species appears to be

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TABLE 2
Parameters for Leaf Development for Various Crop Species (Data Sources with Drastically Different Base Temperature within a Species are Identified)

Plant	t_b	t_{opt}	t_{max}	GDD/ primordium	GDD/ leaf tip	N_o	N_{total}
Leaves		°C					
Maize	8	32	42	20	39	6	8—48
Sorghum a[3,68]	8	26	—	—	48	4	—
b[69]	8	—	—	—	44	—	—
Pearl millet c[70]	12	28+	—	24	26	—	—
b[69]	7	—	—	—	43	—	—
Wheat	0	25	—	—	99	—	—
Barley	1	—	—	—	75	—	—
Rice d[74]	5	—	—	—	90	—	—
b[69]	7	—	—	—	76	—	—
e[70]	7	—	—	—	—	—	—
Cotton	12	32+	—	—	37—41	—	—
Soybean f[81]	7	—	—	—	54	—	—
g[82]	9	—	—	—	55	—	—
h[85]	7	—	—	—	70	—	—
i[83]	9	—	—	—	55	—	—
j[84]	10	—	—	—	—	—	—
k[48]	10	—	—	—	52	—	—
l[86]	4	—	—	—	52	—	—
Sunflower l[86],m[87]	9	—	—	12	29	—	22—29
n[88]	0	—	—	—	38	—	—
Cowpeas	16	—	—	—	30	—	—
English peas l[86]	9	—	—	—	38	—	—
o[8]	3	25	64	—	41	—	—
Faba bean	1	—	—	—	44	—	—
Sugarbeet p[90]	2	—	—	—	30	—	—
q(early trifoliolates only)[91]	1	—	—	—	31	—	—
r[92]	5	—	—	—	29	—	—
Subterranean clover	2	22	42	—	80	—	—
Lambsquarter	15	—	—	—	15	—	—
Pigweed	10	—	—	—	12	—	—
Velvetleaf	8	—	—	—	24	—	—
Cocklebur	6	—	—	—	50	—	—
Banana	8	27	—	—	196	—	—

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TABLE 3
Functions for Duration of Expansion of Individual Leaves

Plant species	Function
Maize	Duration (in GDD_{10} for temp. > 20 and in GDD_7 for temp. <20) = 37.58*N – 1.576*N**2, where N is the leaf number[15]
	Rate of leaf extension for 15<temp. <35 has a tbase of 7°C and t_{opt} of 35 and was nonlinear for temp. <15°C[94]
Sorghum	DUR = LFNO * 16.7[3]
Wheat	t_b for leaf extension = 6°C and t_{opt} = 28°C,[72] or t_b for leaf extension = 0°C and linear to at least 20°C[24]
Sugarbeet	t_b for leaf expansion rate = 7°C[90] t_b for leaf expansion rate = 3°C[91]
Soybean	Duration of expansion of a primary leaf = 70 GDD_{15} with temperature set equal to 23°C if it exceeds 23°C[48]
Faba bean	1/[duration of expansion(d)] = 0.0057 (temp - 1.0)[46]
Cowpea	t_b for leaf expansion = 20°C[89]

the GDD required per leaf tip. Rice had the slowest leaf appearance rates, with 76 GDD_7 per leaf. Sunflower had the fastest rate of appearance, with only 29 GDD_9 per leaf. The others, in increasing order of GDD required per leaf, were maize, pearl millet, and sorghum. These three had 39 GDD_8, 43 GDD_7, and 46 GDD_8 per leaf, respectively.

Cotton and cowpea had greater base temperatures with values of 12 and 16°C, respectively. The GDD per trifoliate for cotton was similar to the grain crops, ranging from 37 to 41 GDD_{12} per leaf. The value for cowpea was lower at 30 GDD_{16} per leaf.

English pea and sugarbeet generally had lower base temperatures than the grain crops. Mean values were 6 and 3.5°C, respectively. The GDD per leaf ranged from 38 to 41 for English pea and from 29 to 30 for sugarbeet at these base temperatures.

A base temperature near 0°C was reported not only for the two winter cereals as expected, but also for faba bean and subterranean clover. The base was 0°C for wheat, 1°C for barley and faba bean, and 2°C for subterranean clover. GDD per leaf was noticeably smaller for the faba bean with 44. Wheat required 99 GDD per leaf, barley required 75, and finally, subterranean clover required 80.

Of the four weed species included, two had high base temperatures, similar to cotton, and two had base temperatures close to 7°C. The two with high base temperatures, lambsquarter and pigweed, required only 12 to 15 GDD per leaf. Velvetleaf and cocklebur required 24 GDD_8 and 50 GDD_6 per leaf, respectively.

B. DURATION OF LEAF EXPANSION

Duration of leaf expansion is strongly related to leaf number for maize[14,15] and sorghum[3] (Table 3). The larger the final leaf area of a leaf, the greater the duration of expansion. Like leaf tip appearance rate, leaf expansion duration has also been shown to be dependent on temperature for several species.

After describing the thermal response of the three systems, leaf primordia initiation, leaf tip appearance, and leaf duration of expansion, it is of interest to know what other factors, such as water or nutrients, can alter these processes. A better appreciation of the effects of such factors should aid in interpretation of errors or model improvement when predicting leaf development in variable field environments.

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C. EFFECTS OF DROUGHT STRESS

Moisture stress, either excess or drought, reduces the rate of leaf extension of maize,[16-18] sorghum,[19,20] sunflower,[21,22] soybean,[21,23] and wheat.[24] However, moisture stress effects on the three processes of leaf development have not been as thoroughly investigated.

The effect of moisture stress on leaf primordia initiation is critical in that altered initiation could change the total number of leaves of a plant and thus the duration of the vegetative phase. Moisture stress prior to panicle initiation has been shown to decrease[25] or increase[20] the final number of sorghum leaves by one to two leaves. Leaf initiation is very sensitive to moisture stress in *Lupinus alba*,[26] barley,[27] and sunflower.[28] Rate of initiation can be halted if drought stress is sufficiently severe.

The effect of drought on rate of leaf tip appearance differs among crop species. Drought has been shown to slow down or stop leaf tip appearance of sorghum,[25] tobacco,[29] and cassava.[30] However, leaf appearance of wheat was 10% faster with dryland treatment than with irrigation.[31] Likewise, leaf appearance of maize can show a short-term delay due to drought, but the effect largely disappears with silking.[32,33] Similarly, drought severe enough to limit leaf area of sunflower to one third of the value of the control had no effect on leaf appearance.[34]

Duration of leaf growth also responds to drought differently depending on crop species. Drought did not alter duration of expansion of wheat.[24] In contrast duration of leaf expansion of sunflower decreased 11 to 22% when drought stress occurred.[34]

D. PHOTOPERIOD, RATE OF CHANGE OF PHOTOPERIOD, AND SOLAR RADIATION

In field environments, associations between photoperiod, cumulative solar radiation, temperature, and a variety of other environmental factors make actual cause and effect relationships difficult to distinguish from spurious correlations. This is especially true for developmental response to photoperiod and amount of solar radiation. However, determination of the true environmental stimulus — photoperiod or amount of solar radiation — causing the plant response is critical for developing models which are general across temperate and tropical regions. For this reason, it is often most appropriate to develop relationships with data from controlled environment growth chambers and validate such relationships with data from field environments. In growth chambers, photoperiods can be extended with low light, thus increasing the accumulated solar radiation only a negligible amount. Likewise, rate of change of photoperiod can be altered without simultaneous changes in cumulative daily solar radiation or changes in temperature as are experienced in the field. Such carefully derived response functions should then be tested for reasonability and accuracy using field data. This aids in avoiding errors in response functions due to artifacts of the growth chamber facility or experimental design.

Another important consideration in deriving relationships between environmental variables and plant developmental processes is the pertinent range for such variables in the field. Care should be taken to ensure that an excessive amount of research effort not be invested in studying plant response to a variable in a range not normally experienced in the field. Photoperiods outside the 10 to 17.5 h range seldom if ever occur in the field environment at times when crop plants are sensitive to photoperiod. Likewise, in temperate regions, daily values for PAR below 3.8 $MJ/m^2/d$ for extended periods only occur in winter periods when temperatures are too low for any measurable development. Typical clear-day values for March to September at latitudes of 30 to 50N are 8 to 15 $MJ/m^2/d$.[35] At latitudes under 30, clear-day values range from 7 to 15 $MJ/m^2/d$ throughout the year. Developmental response functions derived from data with unrealistically low PAR are of limited value for application-oriented plant models.

E. LEAF INITIATION WITH DIFFERENT PHOTOPERIODS AND SOLAR RADIATION

Leaf initiation rate of maize has been shown to have a variable response to photoperiod. In

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a 10 h photoperiod with 2.6 MJ PAR/m²/d, rate was 15 to 19% greater than in a 20 h photoperiod at similar daily PAR.[36] In a similar study, maize leaf initiation rates were 11% smaller in a 12 h photoperiod with 8.7 MJ/m²/d PAR than in a 16 h photoperiod with 11.5 MJ/m²/d PAR.[12]

In a study with very low PAR, leaf initiation rate of cucumber (*Cucumis sativus*) showed no response to incident PAR from 1.2 to 2.3 MJ/m²/d.[37] Only when values for PAR decreased below 1.2 MJ/m²/d was the rate of leaf initiation decreased.

F. LEAF APPEARANCE AND DURATION OF EXPANSION WITH DIFFERENT PHOTOPERIODS AND SOLAR RADIATION

Leaf appearance rate and duration of leaf expansion are more easily measured than leaf initiation rate, and thus have been more frequently studied. Treatments which have been investigated include differences in cumulative daily solar radiation, different photoperiods, and different rates of change of photoperiod. The first two types of treatments will be discussed here, while rate of change of photoperiod will be discussed in a later section.

For maize, the response of leaf appearance rate to photoperiod has varied according to the methods of imposing the treatments. Serial sowings in a greenhouse[38] failed to show a consistent relationship between photoperiod and rate of leaf appearance when PAR exceeded 3.8 MJ/m²/d. In growth chambers,[12] rate of leaf collar appearance in a 12 h photoperiod and with a total PAR of 8.7 MJ/m²/d was 16 to 20% lower than rate in a 16 h photoperiod with a total PAR of 11.5 MJ/m²/d, when temperature was 18°C. However, when temperature was 28°C, there was no significant difference in appearance rate among the photoperiod treatments. Finally, when using field data from several latitudes,[39] leaf tip appearance rate was positively correlated with photoperiod. The mean GDD_8 per leaf when photoperiods were less than 12.5 h was 27% greater than with photoperiods of 15.7 to 16.0 h.

Results with wheat and barley, like those with maize, indicate that the methods of imposing the treatments alter the response of leaf appearance rate. Rate of leaf appearance of barley in growth chambers is constant over a wide range of radiation flux density.[40] Even when flux density treatments were 6-fold different, rate of leaf appearance differed by only 15%. Photoperiod treatments of 8 and 16 h in growth chambers, with nearly identical total light energy, produced little difference in rate of leaf appearance of wheat.[41] However, decreasing illuminance with the same photoperiods caused a systematic decrease in rate of leaf appearance of wheat in growth chambers.[42] Likewise, growth chamber treatments with both greater photoperiod and greater total PAR per day caused an increase in rate of leaf appearance of wheat.[43] Furthermore, results with serial sowings of wheat in Wales showed a strong positive relationship between the photoperiod at seedling emergence and the rate of leaf appearance of barley.[44]

Field results with sunflower indicate that the rate of leaf appearance is sensitive to radiation flux density, but duration of leaf expansion is not.[45] Shading of 50% caused a 11% reduction in rate of leaf appearance. An 80% shading treatment caused a 21% reduction in rate of leaf appearance. Duration of expansion of individual leaves was not affected by these treatments.

Results with faba bean and soybean indicate that the rate of leaf appearance in the former is not sensitive to radiation level, while the latter can be sensitive to either photoperiod or radiation level. In the field, reduction of solar radiation by 56% did not alter rate of leaf appearance or duration of leaf expansion of faba bean.[46] For soybeans in the field, rate of leaf appearance differed by 12% among treatments differing in the radiation level of the artificial photoperiod extension.[47] Likewise, for soybeans in growth chambers,[48] leaf appearance was 14 to 33% slower in a 10 h photoperiod with total PAR of 3.9 MJ/m²/d than in a 16 h photoperiod with total PAR of 6.3 MJ/m²/d. In the same study, leaf appearance in an 8 h photoperiod with total PAR of 3.1 MJ/m²/d was 9% slower than in an 8 h photoperiod with 6.3 MJ/m²/d.

Responses of leaf appearance of forages to increasing photoperiod include decreased rate, no effect, and increased rate, depending on the species. Leaves of tall fescue (*Festuca arundinacea* Schreb.) appeared more rapidly in 8 h than in 16 h photoperiods when both treatments had nearly

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the same total cumulative radiation.[49] Increases in the natural photoperiod from 8 to 16 h had little influence on rate of leaf appearance of ryegrass (*Lolium perenne* L.), but decreased rates of leaf appearance of orchardgrass (*Dactylis glomerata* L.) and meadow fescue (*Festuca elatior* L.) by 13%.[50] In the same study, low light extensions of an 8 h natural daylength with 4 h of low light at each end of the natural photoperiod reduced the rate of leaf appearance of the three species by 12 to 19%. In growth chambers, rate of leaf appearance of orchardgrass and ryegrass were 24 and 8% lower in longer photoperiods of equal energy supply.[51] However, leaf appearance rate of meadow fescue was not sensitive to photoperiod. Rate of leaf appearance of ryegrass, orchardgrass, browntop (*Panicum fasciculatum* Swartz) and paspalum (*Paspalum dilatum* Poir.) increased in response to an increase in photoperiod from 8 to 16 h along with a concomitant doubling of total light energy.[52] Rate of leaf appearance of rye (*Secale cereale* L.)[53] and ryegrass[54] showed no response to the cumulative radiation or photoperiod.

Leaf appearance of cucumber was slower when PAR was below 1.2 MJ/m^2/d.[37] Similar to leaf initiation for this species, there was no noticeable change in rate of leaf tip appearance from 1.2 to 2.3 MJ/m^2/d.

In several field data sets with bananas (*Musa* sp.), leaf appearance rate in a 14 h natural photoperiod was 25% faster than the rate in a 10 h natural photoperiod.[55]

G. LEAF APPEARANCE WITH DIFFERENT RATES OF CHANGE IN PHOTOPERIOD

Rate of change of photoperiod has been found to be correlated with leaf appearance rate of wheat and barley in the field.[56-58] However, controlled environment research has failed to support this as a cause and effect relationship. An experiment in controlled-temperature growth chambers indicated that rates of change of photoperiods of +5 min/d, -5 min/d or no change had no effect on leaf appearance rates of two wheat cultivars and two maize hybrids.[59]

H. NUTRIENTS

Nitrogen stress for the most part does not seem to alter rate of leaf appearance of forages. The general conclusion in a review on leaf appearance rate of grass species was that there was no noticeable response of leaf appearance rate to mineral nutrition.[60] Rate of leaf appearance of timothy (*Phleum pratense* L.) was not influenced by the level of nitrate in the culture solution used.[61] Different levels of nitrogen nutrition in the culture solution did not alter rate of leaf appearance on the main shoot of rye plants.[53] Nitrogen deficiency sufficiently severe to stop tiller formation of ryegrass had no effect on the rate of appearance of the leaves.[54]

However, for some crops it appears that nitrogen stress can alter leaf appearance. When the radiation intensity was sufficiently great, the leaf appearance rate of wheat was decreased 29% by nitrogen stress.[62] Likewise, leaf appearance rate of soybean fertilized with only 3 m*M* of N in solution was 13% below the rate of soybean fertilized with 18 m*M* of N in solution.[48]

I. WITHIN-SPECIES CULTIVAR DIFFERENCES

In any modeling effort, when attempting to simulate a crop species across a wide range of latitudes and regions, cultivar differences should be investigated. Such differences for leaf appearance rates exist in some common crop species. Leaf initiation rate of maize cultivars has been found to differ by as much as 12 to 16% from the mean value.[63] Likewise, rates of leaf appearance of different maize cultivars could vary by as much as 12 to 16% from the mean.[64] The GDD per leaf of some cotton cultivars can be as much as 6 to 8% different from the mean.[65] Leaf appearance rate of soybean cultivars can vary by as much as 28%.[48]

III. SUMMARY

The majority of plant species in this chapter can be categorized into three groups depending

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on their base temperatures for leaf development. The most extensive group has base temperatures of 7 to 9°C. These species include maize, sorghum, pearl millet, rice, soybean, sunflower, English peas, velvet leaf, and banana. From an application viewpoint, GDD with a base temperature of 8°C could be used for all of these. The second group, with base temperatures of 0 to 2°C, includes the winter cereals wheat and barley, as well as faba bean, sugarbeet, and subterranean clover. As with the first group, a single base temperature value should be adequate. The intermediate value of 1°C is the obvious choice. Finally, the group with base temperatures of 12 to 16°C includes cotton, cowpeas, and lambsquarter. The average base temperature for these is 14°C.

The impact of environmental factors other than temperature on leaf appearance is unresolved and appears to vary with species. Drought retards leaf appearance of sorghum, tobacco, and cassava, but such an effect is not evident for wheat, maize, and sunflower. Radiation flux density appears to have no effect on leaf appearance of maize, barley, and faba bean. In contrast, decreases in flux density slowed leaf appearance of soybeans and sunflower. Reported effects due to photoperiod and rate of change of photoperiod are difficult to verify at this time due to frequent confounding by temperature and total daily PAR. Likewise, while a range of genotypes within a species can often be chosen which will demonstrate within-species variability in leaf development, future research may show that the majority of commercial cultivars within each crop species can be simulated with a single GDD system.

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Chapter 6

STEMS: PATTERNS AND DURATION OF DEVELOPMENT

J. D. Hesketh, K. Wisiol, W. T. Pettigrew, and D. M. Alm

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I. QUANTIFYING STEM GROWTH AND DEVELOPMENT

Stems vary greatly in form, function, and utility (Figure 1).[1] Stem material can be harvested as stored sucrose (sugarcane, sweet sorghum, corn, sugarmaple) or other by-products (rubber, resins, turpentine), for wood, for fiber (flax, hemp, jute, kenaf, ramie), or for food, as tubers (potatoes) or stalks (kohlrabi, celery).

Many cactii and succulents have water-storing stems that behave like leaves, with the real leaves modified into spines or other organs. Some orchids have swollen water-storing stem portions called pseudobulbs. Modified stems, such as stolons, tillers, corms, rhizomes, and the stem parts of buds or bulbs, can be important in vegetative reproduction or overwintering and can provide additional support for the main stem, as tendrils do.

As we describe in this chapter, the stem apical and axillary meristems determine the potential pattern of growth, and the supply of materials coupled with the effect of temperature on growth rates determine how this pattern is implemented. Stem buds can give rise to new shoots, branches, flowers, or roots. In addition to providing mechanical support for a canopy of leaves and reproductive organs, stems also contain vascular tissue for transport of water, nutrients, and growth regulators among plant tissues or organs.

These introductory comments hint at the problem plant growth modelers face when attempting to modify existing models for predicting growth and development of a species or cultivar, or when trying to develop a general model with adjustable coefficients for the same purpose. For obvious reasons, foresters have studied and modeled stem behavior in detail; agronomists have neglected the stem in their research and models. Horticulturists and weed scientists are bothered more by this problem than are crop scientists because of the diversity of species they must work with. We address the problem here by searching for general classes of stem behavior that can be represented in widely grown, well-studied species.

As phenologists or modelers, we emphasize the research aspects of a model, or a system of postulates, data, and inferences presented as a mathematical description of how an organism behaves. We are interested in rates of development as a function of thermal time or degree days, in nutritional budgets, and in response mechanisms controlling the initiation of organs and the onset of dormancy, abortion, or budbreak. Such an approach makes new demands upon how we define the growth and developmental aspects of morphology (form and structure), or morphogenesis (structural changes in development).

General texts and reviews of anatomy of common plants [2-33,65,69-71] are used as sources. Our list could be extended to include similar sources for other crops, weeds, grasses, and horticultural plants. The authors are not expert anatomists; the following is a general summary of stem growth and morphogenesis which should be useful to agronomists, horticulturists, and foresters. A few sources are cited as essential for further study. Gray's[15] 1887 text is a useful and interesting example; the development of crop growth and yield models has forced many of us to go back to anatomical or morphological basics that have long been ignored.

We discuss stem growth and developmental morphology in relation to phenology, the science dealing with effects of climate on periodic biological phenomena. As defined by Nuttonsen,[34] "such phenomena include dates of sowing, germination, emergence, tillering, leaf bud opening, shooting, blossoming or heading, terminal bud formation, and various distinct stages of biological or market maturity — for appropriate organs for genetically homogeneous clones or cultivars".

In a distinction defined by Dahl and Hyder,[8] growth is an irreversible increase in size that is quantitative in nature, whereas development involves qualitative changes in form, structure, and general state of complexity of the plant. Furthermore, they state, citing Beard,[4] that developmental processes involve cell division, differentiation, and morphogenesis. We hope to quantify these changes in form, structure, and general complexity with respect to dimensions, nutrients, heat, and time. At some points in this process the distinction between growth and developmental processes may blur.

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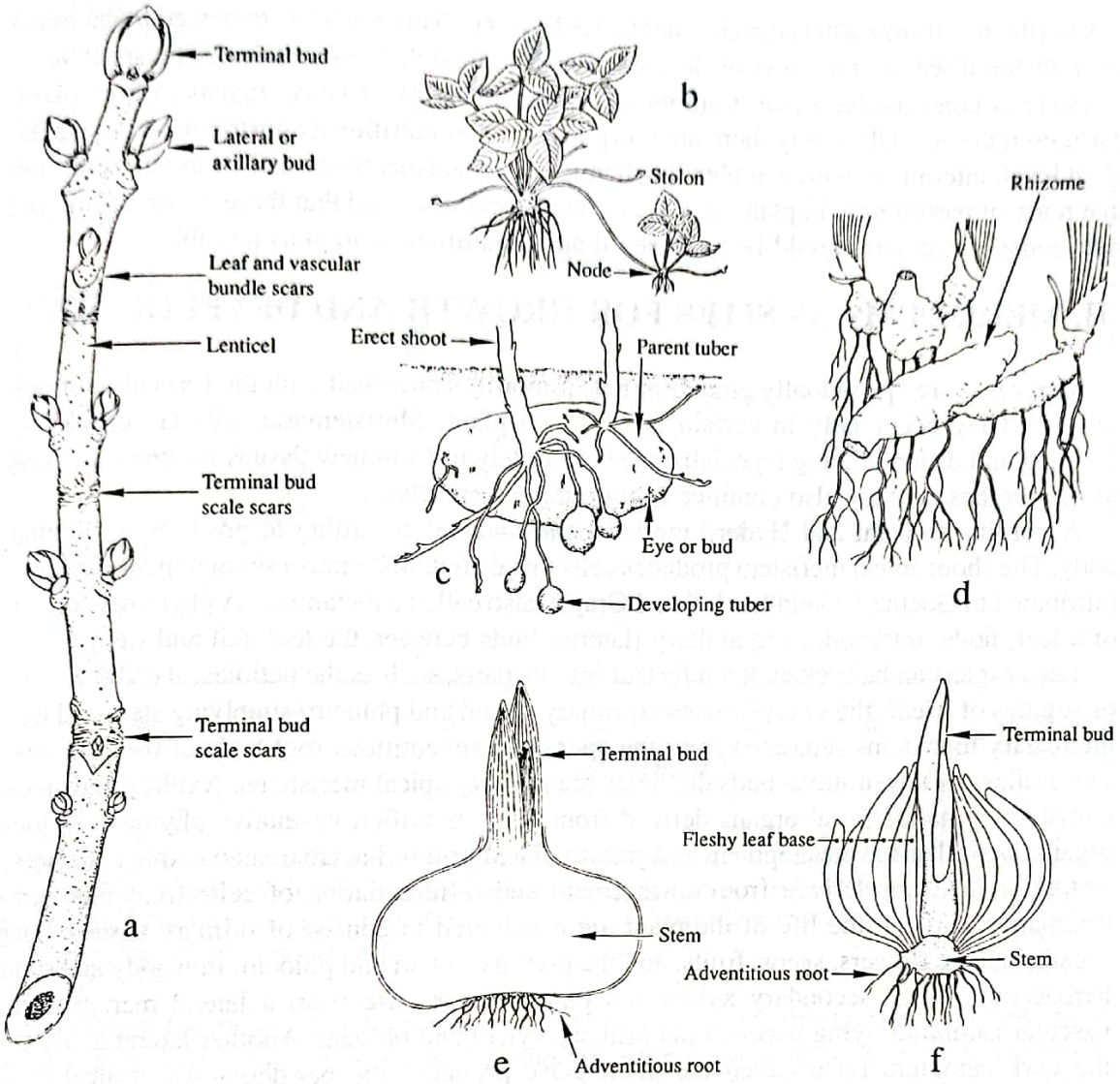

FIGURE 1. Some examples of stems: (a) woody stem of buckeye, *Aesculus* sp., dormant stage; (b) stolon of strawberry, *Fragaria* sp.; (c) tuber of potato, *Solanum tuberosum* L.; (d) rhizome of *Iris* sp.; (e) corm of *Gladiolus* sp.; and (f) base of onion bulb, *Allium cepa*. Similar information can be found in Gray.[15] These examples indicate the types of stem behavior with which a modeler of weeds or horticultural plants must deal. (From Bold, H. C., *The Plant Kingdom*, 3rd ed., Prentice-Hall, Englewood Cliffs, NJ, 1970. With permission.)

Approaching the analysis of growth and development through the quantification of morphogenic and phenological processes provides a base for studying how nutrients are partitioned, how plant growth regulators function, how plants senesce, and how plants might respond to global atmospheric increase in CO_2 or an environmental stress. This approach is needed to define any system under study. Floral physiologists have used parts of this approach for many years for an obvious reason: a plant is committed to flowering long before the first flower bud becomes visible to the naked eye. Dosage response experiments, without some analysis of nutritional budgets, phenology, growth and morphogenesis, and interactions with temperature, are of limited scientific value.

Watson and Casper,[33] reviewing "morphogenic constraints on patterns of carbon distribution in plants", underscored these points. They stated that "phenotypic plasticity is an important element in the response repertoire of plants. It may be manifested as changes in organ morphology as well as in patterns of biomass distribution. Morphological plasticity throughout growth is possible because plant development is modular in form. Growth results from the reiteration of basic morphological subunits produced by meristems. Because meristems may develop into either reproductive or vegetative structures, patterns of biomass distribution

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reflect (the results of earlier) developmental (behavior)." These authors reviewed much of the same material we do, for some of the same reasons, though from a different perspective.

There is considerable interest among the biochemical plant physiologists in how plants partition nutrients. Obviously there are morphogenic and nutritional constraints at the whole-plant level, intermixed with complex biochemical mechanisms controlled by genes. It follows that nutrient partitioning in plants is a very complex process, and that these morphogenic and nutritional constraints should be understood and quantified as soon as possible.

II. MERISTEMS AS SITES FOR GROWTH AND DEVELOPMENT

Meristems are "perpetually young tissues, primarily concerned with the formation of new cells".[11] They occur only in certain parts of the plant. Meristematic cells are capable of dividing and differentiating (specializing) indefinitely to form new tissues leading ultimately to new organs, as they also continue to reproduce themselves.

According to Dahl and Hyder,[8] meristems are named according to position in the plant body. The shoot apical meristem produces cells that differentiate into a shoot unit, or phytomer (attributed to Goethe,[35] Gaudihard, [35] and Gray[8]), also called a metamer.[33] A phytomer consists of a leaf, node, internode, and axillary (lateral) buds between the leaf axil and stem.

Each organ can be broken down further into its parts, such as the petioles, sheaths, ligules, or stipules of a leaf; the vascular tissue (primary xylem and phloem) supplying stem and leaf; intercalary meristems separated from the apex; and adventitious root buds of the internode. The axillary or adventitious buds duplicate the primary apical meristems. Axillary and apical meristems produce floral organs derived from many modified vegetative phytomers (floral organs, as well as the development and growth of leaf primordia, are treated in other chapters).

Organs that are derived from enlargement and differentiation of cells from meristems originating early in the life of the plant are considered to consist of primary tissues. Such organs include flowers, seeds, fruits, and the primary xylem and phloem. In woody and some herbaceous plants, secondary xylem and phloem later arise from a lateral meristem, the vascular cambium, lying between the primary xylem and phloem. Another lateral meristem, the cork cambium (also called the phellogen), produces the periderm, the cortical outer protective layer of many stems and roots. In general, monocots lack a cambium.

Intercalary meristems, separated from primary meristems by maturing tissue, occur at internodes, the leaf base in monocots or the petiole base in dicots. They produce primary tissue for elongation. Best known are the intercalary meristems at the base of the internode, blade, and leaf sheath in grasses and many other monocots. However, intercalary growth occurs in all plants having nodes and internodes. Comparable growth regions in the cortex of roots and woody stems are sometimes called rib meristems. Unlike true meristems which may develop indefinitely, intercalary meristems have a fixed course of development, and ultimately become mature tissue.

III. THE SHOOT APEX

The shoot apex is made up of four regions, described here in a close paraphrase of Dahl and Hyder[8] and Romberger.[27] The distal region is the summit of the apical dome, including apical initial cell groups. Below this is the subdistal region where primordia are initiated and metabolites conducive to growth have accumulated, but in which no obvious morphological changes have taken place. Below this is the organogenic region where obvious outgrowth of leaf primordia occurs and tissue differentiation becomes detectable. The boundary is indistinct between the organogenic region and the subapical region below it, where continued primordial enlargement, considerable widening and elongation of the internode, and continued differentiation of the vascular tissue occur. Below all this is the region of maturation (completion of growth) with its obvious role in phytomer growth and development.

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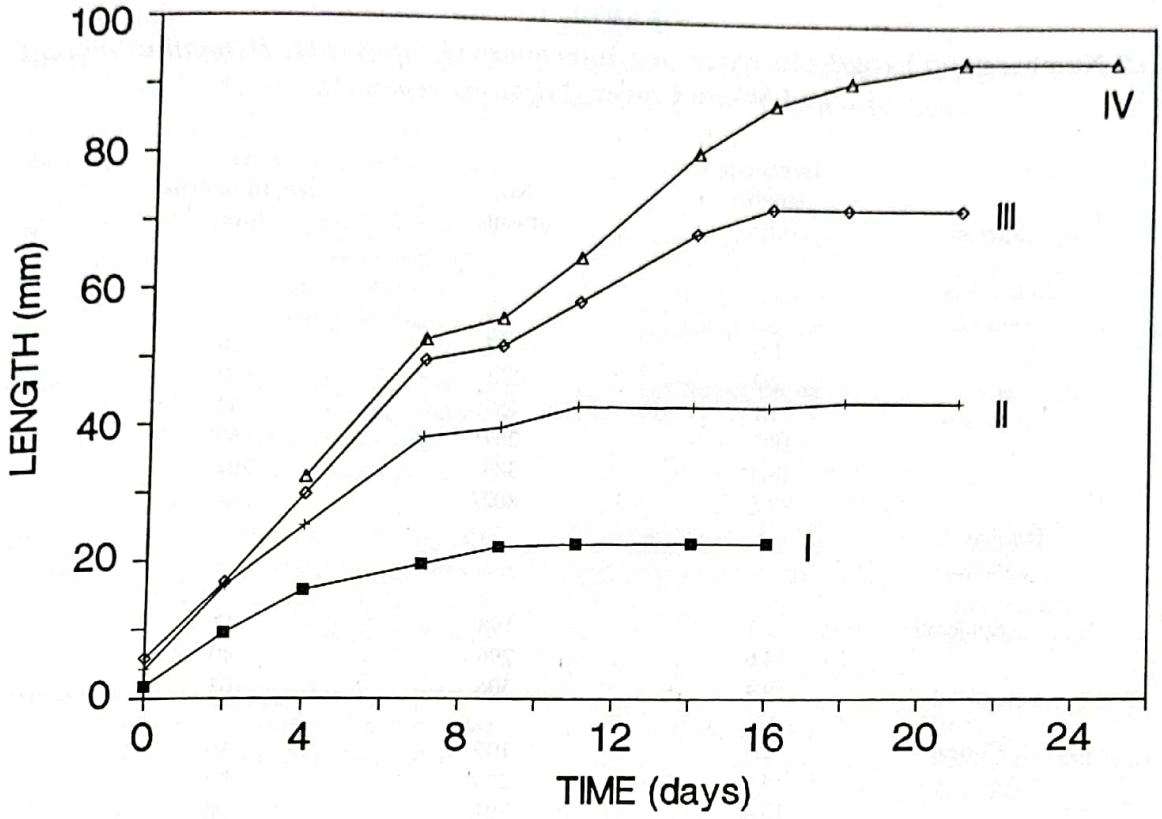

FIGURE 2. Growth of divisions of the first internode of a *Helianthus annuus* L. (sunflower) seedling. The internode was marked into 3 equal parts (I-III) on day 1, when 6 mm long, with a 4th part (IV) added on day 4. From Wetmore and Garrison.[36] These data reflect the state of the art of research on internode growth dynamics until recent work on *Trifolium*; Table 1 details both data sets.

We discuss the growth and development of stems in relation to this terminology later in the chapter. In order to obtain a better understanding of the subject matter involved, one might begin study with Dahl and Hyder,[8] proceed through Cutter,[6] and then consult the standard plant anatomy texts.[11-13] Precise definitions for the associated terminology are essential for understanding some of this material.

IV. INTERNODE ELONGATION

As mentioned previously, elongation of the stem portion between nodes is an example of intercalary growth (growth localized in regions between base and apex) via meristems separated from the apex by more mature tissue. During early growth in grasses and many other monocots, internode growth is concentrated near the shoot base in a stem section called the crown, which is composed of successive phytomers with short internodes. Such plants build up photosynthetic capacity (leaf tissue) and reserves before producing the longer internodes that begin to appear after floral initiation (FI) at the shoot apex. All internodes quickly reach their maximum diameter, since no cambium cells are present. However, in some monocots such as palms (Palmae family) a diffuse meristematic region beneath the leaf primordia can produce secondary growth that thickens the stem,[11] and internodes elongate only after the stem becomes rather wide.

A. CELL LEVEL

Cell enlargement and division play varying roles in primary internode extension and diameter increase in primary tissues.[11] Extension of an internode of sunflower (*Helianthus annuus* L.) is graphed in Figure 2; the numbers and lengths of cells in a *Helianthus* internode[36]

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TABLE 1
Cell Numbers and Lengths in Extending Internodes of Sunflower, *Helianthus annuus* L., and White Clover, *Trifolium repens* L.

Species	Internode length[a] (mm)	No. of cells	Av. length of cells (μm)
Helianthus annuus L.			
	1.5	77	20
	2.2	111	20
	5.1	155	33
	18.3	267	69
	78.3	383	204
	99.5	402	248
Trifolium repens L.			
Epidermis	2.1	198	11
	14.6	296	49
	19.4	306	65
Cortex	2.1	109	19
	14.6	203	72
	19.4	191	106
Pith	2.1	112	19
	14.6	228	69
	19.4	211	97

Note: Helianthus data from Wetmore and Garrison.[36] *Trifolium* data from Thomas.[30]

[a]Lengths are for extending internodes or, in the case of the final lengths given, fully extended internodes.

and in *Trifolium repens* L. internode tissues (epidermis, cortex, and pith)[30] are shown in Table 1. As the internode extended some 65-fold in *Helianthus*, there was a 5-fold increase in cell numbers in longitudinal rows in the pith and a 13-fold increase in average cell length. In *Trifolium*, extension of internodes from 2.1 to 14.6 mm resulted in only 1.5 times as many cells but average cell length increased 4.5-fold (Table 1).[30] However, a comparable set of measurements in lilac, *Syringa vulgaris* L.,[29] showed cell number increasing some 65-fold while cell length increased only 3-fold. Thus, in some species and growth stages cell enlargement is more important for internode elongation, while in others cell division is more important.

New growth in these dicots is added at the top of the internode as it extends. In grasses and other monocots, new growth typically progresses from the base of the extending internode. For example, Bleecker et al.[73] identified three zones of growth and development in an elongating rice (*Oryza sativa* L.) internode: (1) the intercalary meristem at the base of the internode where cell division and elongation takes place, (2) a zone of elongation without division, and (3) a zone of differentiation where neither division nor elongation takes place. Kende[74] reviewed an associated five-year effort on this system at the anatomical, physiological, and biochemical levels.

Dwarfing genes result in shorter internodes in pea (*Pisum sativum* L.),[36-37] corn (*Zea mays* L.),[38] sorghum (*Sorghum bicolor* (L.) Moench),[39] wheat (*Triticum aestivum* L.),[40] and rice.[41] Application of gibberellins will cause internodes in dwarf peas to elongate normally during growth, while gibberellin inhibitors will suppress internode elongation in normal pea plants; endogenous gibberellin concentrations during internode elongation are correlated with final

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TABLE 2
Main Internode-Length Phenotypes of Pea (*Pisum sativum* L.) Determined by the Five Loci Le, La, Cry, Na, and Lm[37]

Phenotype	Phenotype description	Genotype	Ref.[a]
Tall	Normal long internodes above 4, internodes 5-6 onwards approx. 0.1 m, probably wild-type	Le La Cry Na Lm Le La cry^c Na Lm Le La cry^s Na Lm Le la Cry Na Lm	Mendel, 1866 White, 1917
Dwarf	Internodes 40—50% of tall types, zig-zag appearance of stem; pleiotropic effects on flowering	As for tall except le	Mendel, 1866 White, 1917
Nana or Compactum	Extreme shortening of internodes (usually less than 0.01 m), darkly colored leaves, reduced yield	As for tall and dwarf except na	Wellensiek, 1969, 1971 Reid, Murfet, and Potts, 1983
Cryptodwarf	Long, thin lower internodes, higher internodes still larger than dwarf type	Le la cry^c Na Lm Le la cry^c na Lm	Rasmusson, 1927 Potts, Reid, and Murfet, 1985
Cryptotall	Long, thin lower internodes, but above node 7 slightly shorter than tall type	Le la cry^c Na Lm	Reid, Murfet, and Potts, 1983
Slender	Long, thin stems from node 0, pale foliage, malformed flowers, parthenocarpic pods, and reduced yield	Le la cry^s Na Lm le la cry^s Na Lm Le la cry^s na Lm le la cry^s na Lm	de Haan, 1927, 1930 Potts, Reid, and Murfet, 1985
Macrodwarf Microcrypto-dwarf Microslender Microtall	Smaller than corresponding dwarf, tall, crypto-dwarf or slender types in all parts including internode length	As for corresponding dwarf, tall, cryptodwarf or slender, except lm	Rasmusson, 1936 Lindqvist, 1951

[a] See Murfet and Reid[37] for full references.

internode length.[36] Internode-length phenotypes and genotypes of pea are given in Table 2; Table 3 shows the response of different lines to gibberellins.

B. ORGAN LEVEL

For positioning leaves in the canopy (height above the ground) and for studying the nutritional requirements of an internode or a phytomer, it is important to know how the internode grows in length and weight in relation to other phytomer components for well-defined plant systems. It is also helpful to plot dimensions and weights of phytomer components against growth stages to overcome temperature effects on growth rates. One then must be able to predict growth stage as a function of a degree-day or thermal-time relationship.

In the Leaf Plastochron Index (LPI) method of numbering leaves, successive leaves are given positive numbers if below a reference leaf and negative numbers if above. Larson[43] used

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TABLE 3
Sensitivity to Gibberellin (GA1) and to Gibberellin-Synthesis Inhibitors AMO1618 and PP333, with Levels of Endogenous Gibberellins, in Differing Internode-Length Genotypes of Pea (*Pisum sativum* L.)[37]

Gene or mutant line	Phenotype	Sensitivity to GA1	Sensitivity to AMO1618 and PP333	Endogenous GA levels
le	Dwarf	High	High	Low GA1, others normal
na	Nana	High	Medium	All low
la cryc	Crypto	Medium	Medium	Normal
la crys	Slender	Low	Low	Normal
lm le	Microdwarf	High	High	Unknown
K202	Nana	High	High	All low
K511	Dwarf	High	High	All low
JI 1420	Erectoides	Low	Unknown	Normal

the index units as physiological time units in comparing internode elongation with that of leaves (primordia, laminae), petioles, and stipules in cottonwood (*Populus deltiodes* Bartr.) (see Figure 3). Internode lengths lagged behind those for the other phytomer components.

Malvoison[44] extended this analysis to a succession of wheat mainstem phytomers; we show his measurements for components (blade, sheath, internode) of the sixth phytomer, with some of his data for elongation of the head, in Figure 4. Once again, internode lengths lagged behind those for the other phytomer components, including the sheath, which eventually enclosed the fully extended internode. His measurements included plant-to-plant variability associated with the destructive dissection of plants sampled; Larson's method described previously involved measurements on the same plant.

Hesketh et al.[45] measured leaf area, along with internode and sheath lengths and associated dry weights, for phytomers of a corn shoot; some of these values for the 13th phytomer on the stalk, just below the ear node, are shown in Figure 5. To obtain such values, frequent measurements were made on dissected plants harvested from carefully spaced plant populations.

As an approximation for the logistic course of internode weight with V-stage (a growth stage unit obtained from the number of the stalk node showing the youngest collar), as illustrated in Figure 5, regression coefficients for internode weight vs. V-stage for different phytomers on the corn stalk are plotted against the final weight attained (Figure 6). Nodes above the one showing the maximum final weight accumulated dry matter faster than those below, but for a shorter duration.

One needs the regression intercept as well as the effective duration (final weight divided by the weight accumulation rate) of linear dry matter deposition for predicting dry matter accumulation in a stalk. Hesketh et al.[45] summarized information for the appearance, growth duration and rate, and completion of growth for components of phytomers on the corn stalk. Such information provided a base for predicting the growth of a crop canopy as well as how the growth of the canopy is integrated with that of the reproductive organ, particularly during the seed-set stage. Effects of plant spacing, drought stress, and experimental site on components of the 13th corn soybean are shown in Table 4. The final harvest was at silking; stalk weights can still fluctuate after silking, but maximum weights occur about 1 week later.

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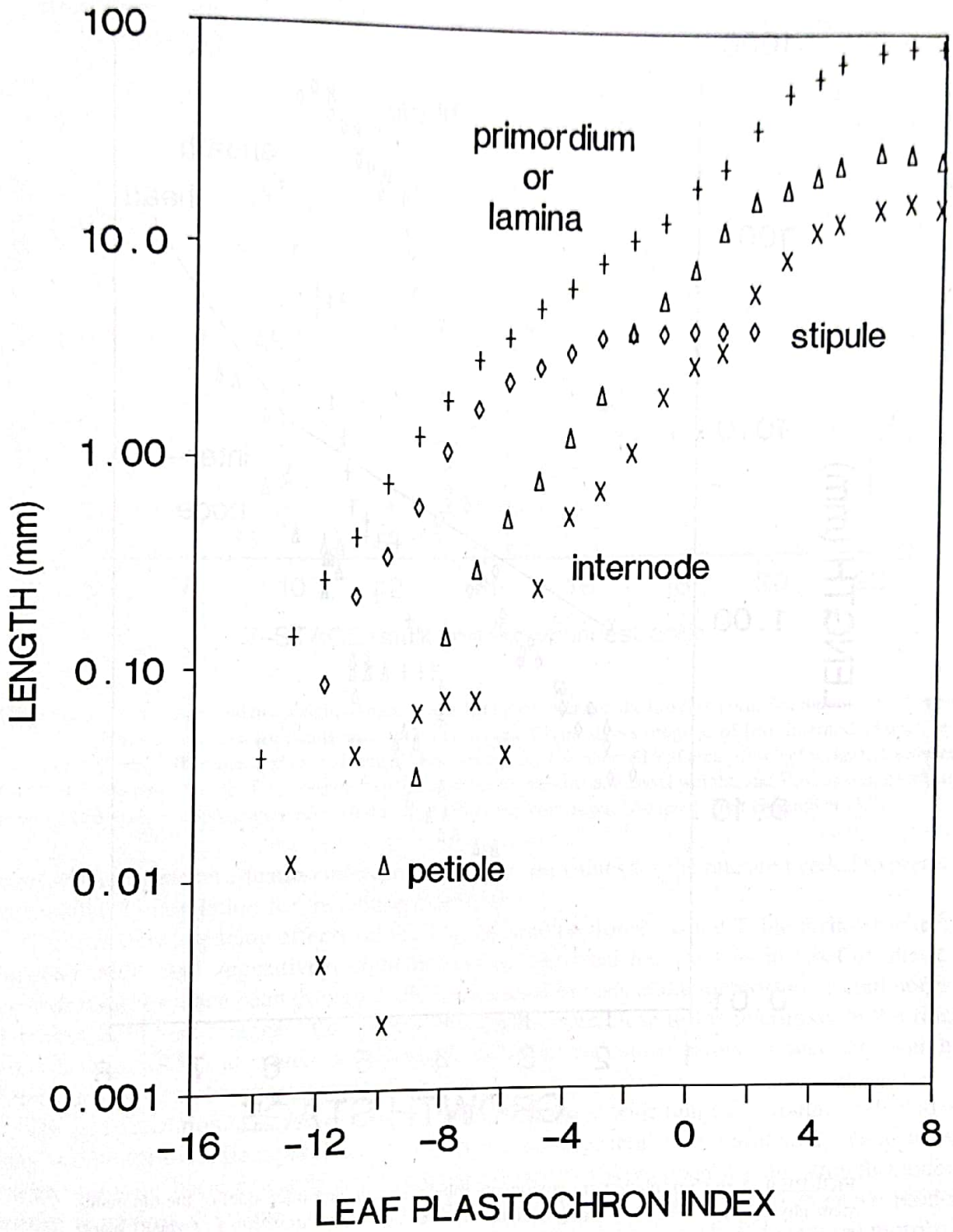

FIGURE 3. Length of phytomer parts in a dissected *Populus deltoides* Bartr. (cottonwood) shoot with 23 leaves, by LPI. LPI ranges from -14 to + 8, from the youngest leaf primordium at the shoot apex down the mainstem, with position of the reference leaf defining LPI = 0. The values reflect growth rates that would hold if all phytomers eventually attained the same dimensions. (From Larson, P. R., *Am. J. Bot.*, 62, p. 1984, 1975. With permission.)

Cao et al.[77] reviewed the use of logistic, Gompertz, and Richards functions for quantifying organ growth; after consideration of these functions Reid et al.[58] used linear equations to quantify leaf expansion among a succession of phytomers. Alm[78] subsequently used the logistic equation for the same purpose. Our regression coefficients were satisfactory (Figure 6), but these other functions eliminate the need for specifying when to start linear growth after an organ appears.

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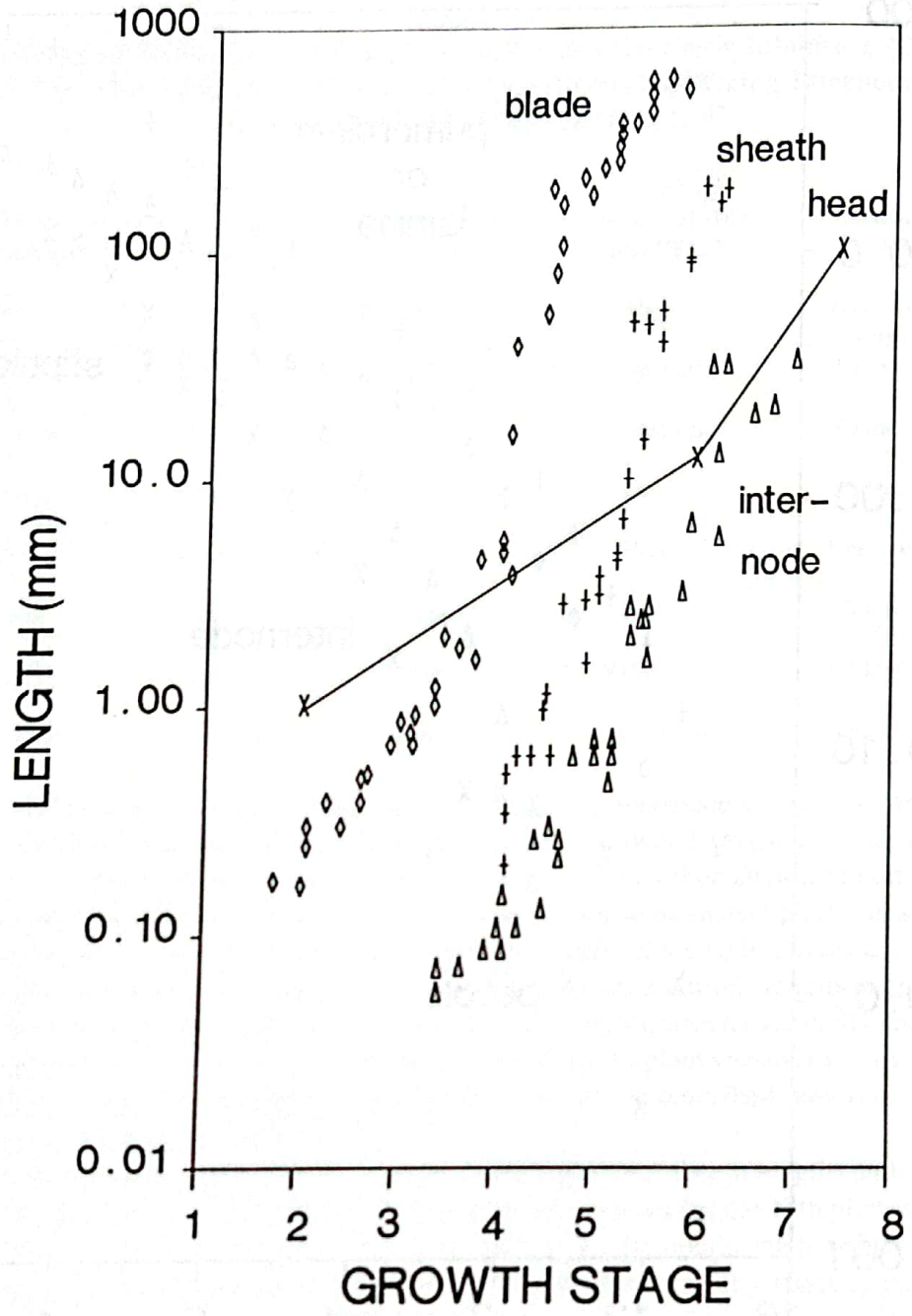

FIGURE 4. Length of phytomer components (blade, sheath, and internode) of the 6th mainstem phytomer, as well as the length of the head of a *Triticum aestivum* L. (wheat) plant. Growth stages were substituted for calendar time, thereby taking into account temperature effects on growth. A thermal model is needed to predict timing of the growth stages. (Adapted from Malvoison.[44]) (*Agronomie* is a good source for related information.)

Hesketh et al.[46] made similar dimensional and weight measurements in soybean (*Glycine max* (L.) Merr.); results for the 7th phytomer in one cultivar (BSR-201) are shown in Figure 7.[46] The increase in internode weight for this phytomer with each successive V-stage (approximated with the number of mainstem leaves longer than 1 cm above the unifoliolates) seems to be more even than for the corn data shown in Figure 5; regression coefficients for changes in internode weight in early and late maturing soybean cultivars are shown in Figure 8. In soybean the nodal-position effect is much more pronounced; internodes higher on the plant have more rapid dry matter accumulation rates relative to the final weight attained. As for the

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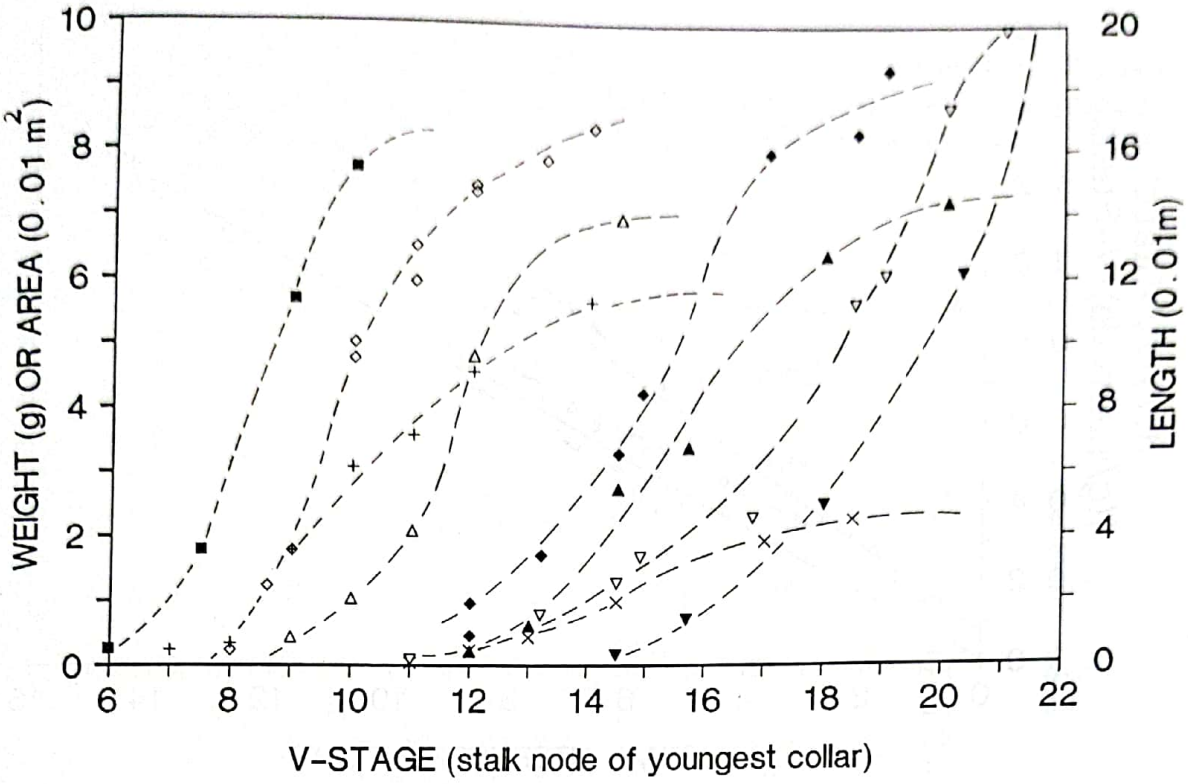

FIGURE 5. Dimensions and dry weight of parts of the 13th phytomer and the tassel of corn, *Zea mays* L. cv. Pioneer 3377, just below the ear leaf, for plants with 19.5 total leaves. Graph shows progress of leaf, internode, tassel, and ear by growth stage. ■ = total leaf area, emerged and unemerged; + = emerged leaf area, ◇ = leaf weight, Δ = sheath length, ◆ = internode length, ∇ = internode weight, × = sheath weight, ▲ = tassel weight, and ∇ = ear weight. Plants were spaced every 0.23 m within a row and every 0.76 m between rows. (Adapted from Hesketh et al.[45])

corn stalk, regression equation intercepts and duration values for the rate are needed to predict dry matter accumulation for the entire mainstem.

Table 5 shows spacing effects on the 7th soybean phytomer, while Table 6 shows effects on total nodes and vegetative weight produced. The final harvest was just before the R5 growth stage, or when bean growth could be detected in pods at the topmost mainstem nodes. The data in Figure 7 suggest that internode weights were close to the maximum at the final growth stage (R5+) at which we sampled, although of course errors in such dry weight determinations can be considerable.

The generalization that crop plants yield the same over a wide range of population densities may suffice for most field predictions; however, such a generalization ultimately needs to be backed up with basic research and synthesis. If one has developed a plant growth model, testing it against data from a plant population study may enable one to improve model prediction in other situations. Few plant growth models contain logic based upon the morphogenic detail that we present or cite here. In most models, stems are allocated a fixed fraction of available nutrients. An exploratory effort was made, when developing logic for the cotton (*Gossypium hirsutum* L.) model COTCROP,[47] to include some details about how a phytomer develops and grows. The quantitative aspects of phytomer ontogeny have been neglected for too long; detailed models based upon the information described previously are needed to answer some of the environmental questions we now face.

V. VASCULAR TISSUE

New vascular tissue, which transports water, nutrients, and growth regulators, is produced at the shoot apex. In herbaceous plants this tissue is commonly organized into vascular

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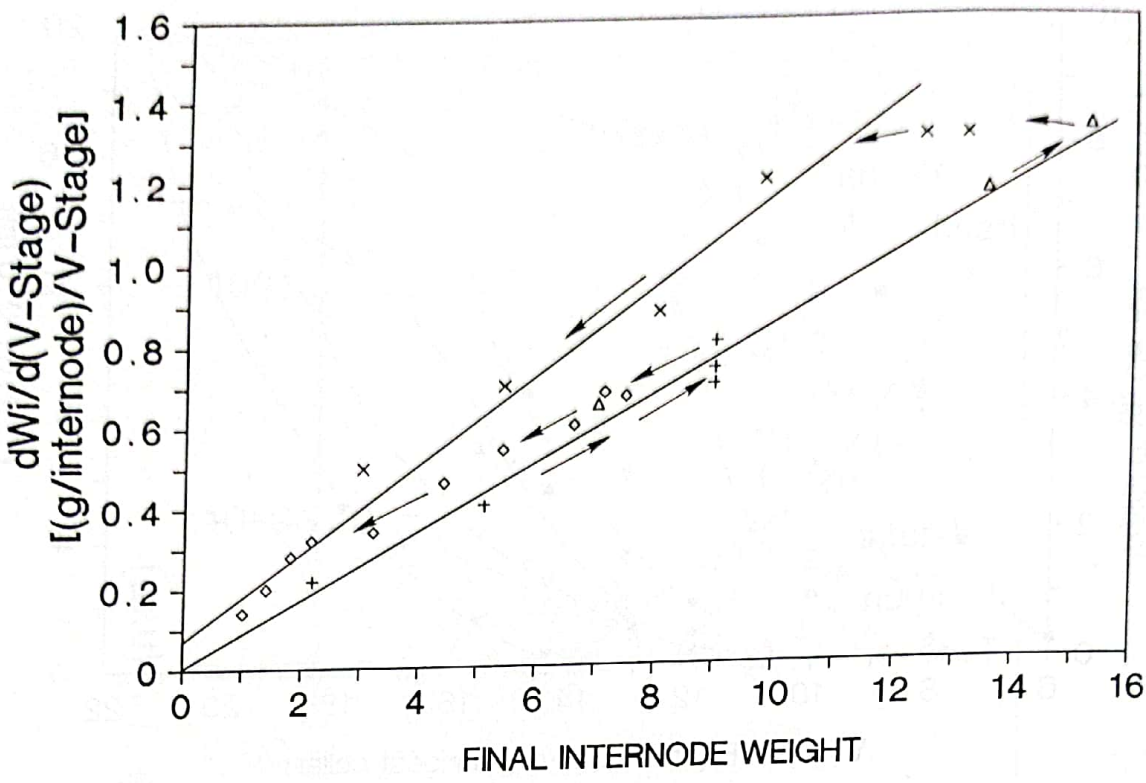

FIGURE 6. Rates of corn internode dry matter accumulation per V-stage (regression coefficients calculated from dry weight values of specific internodes at different stages of growth, such as shown in Figure 5, with emphasis on the values measured during the linear phase of logistic growth) plotted against the internode dry weight measured during silking. V-stage was determined by the number of the highest node showing a leaf collar. New Zealand results (Δ for the heaviest internode and below, × for internodes above the heaviest one) were for Palmerston North plants spaced every 0.21 m within the row; the average R^2 for nodes 6 to 14 was 0.94, average n = 7. Urbana results (+ for the heaviest internode and below, ◊ for internodes above the heaviest one) were for plants spaced 0.23 m apart within the row; the average R^2 for each point being 0.87 with the average n = 24. Arrow direction denotes increasing height on the stalk. Corn rows were 0.76 m apart. Further experimental details are given in Table 4 and Hesketh et al.[44] The V-stage axis intercept where dry matter started to accumulate at a linear rate was estimated for each internode; these intercepts usually were one V-stage earlier than that for the phytomer.

bundles.[11] These are strands containing xylem, phloem, and other tissue. Vascular bundles are arranged in a ring near the outer surface of the stem in many plants. In stems of monocots the bundles are often dispersed throughout, as in corn and sorghum, but in some monocots such as turfgrasses they are arranged in one or several concentric rings.[7]

Secondary vascular tissue is produced later by woody plants and some herbaceous plants via a cambium, meristematic cells between the primary xylem and phloem. The amount produced ranges from entire rings, as in trees, to separate stands, to nothing, depending upon the species. Few monocots exhibit cambial growth; exceptions include species of Agave, Yucca, and Aloe.[11]

A. PHYLLOTAXY AND VASCULAR INTERCONNECTIONS BETWEEN LEAVES

Primary vascular tissue of the stem extends to the vascular system of the leaf via bundles constituting leaf traces, but the relation of the development of the two vascular systems is unclear.[11] Larson[43,48,49] showed how procambial vascular tissue (traces seen in microscopic sections) enters the base of the apical dome and penetrates developing leaf primordia of a cottonwood shoot. He concluded that one can still only speculate about how the two growth processes are integrated.

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TABLE 4
Weight and Length of Components of 13th Phytomer of Corn (*Zea mays* L.) Plants at Different Spacings, Water Stress Levels, and Locations (plants at different spacings were sampled at anthesis; plants in an irrigation study were sampled at the times given)

	Internode			Leaf		Sheath	
Treatment	W (g)	L (cm)	W/L (g/cm)	W g	W/Area (g/dm²)	W (g)	W/leaf area (g/dm²)
Within-row							
Open-spaced	6.9	13.6	0.51	6.6	0.90	3.9	0.53
0.305 m	6.9	16.5	0.42	5.9	0.78	3.0	0.39
0.23 m	5.8	15.7	0.37	5.4	0.75	2.7	0.38
0.153 m	3.1	13.6	0.23	4.8	0.69	2.0	0.29
0.10 m	2.0	13.3	0.15	3.8	0.60	1.5	0.23
Irrigation							
Control-0 DBS*	4.4	12.9	0.34	4.4	0.69	2.7	0.42
3 DBS	4.3	13.1	0.32	4.5	0.73	2.5	0.40
7 DBS	5.0	15.2	0.33	4.7	0.72	2.6	0.41
15 DBS	5.5	17.1	0.32	4.5	0.73	2.5	0.40
21 DBS	6.5	18.6	0.35	4.2	0.72	3.4	0.57
S.E. (n = 3)	0.37	3.3	0.002	0.18	0.018	0.133	0.016
Location							
Urbana, IL (0.2 m space)							
April 28	5.0	18.8	0.26	5.9	0.69	2.7	0.32
May 14	4.5	18.1	0.25	5.6	0.69	2.7	0.33
Palmerston North New Zealand							
Open-spaced	9.3	13.4	0.70				
0.24 m space	8.5	16.3	0.52				
0.21 m space	6.0	16.0	0.38				

W = mass in g, area = leaf blade area in 0.01 m² (dm²), L = length in 0.01 m (cm); DBS = days before silking that irrigation treatment was imposed. Planting dates and cv.: for spacing study May 6, 1988, Pioneer 3377; irrigation study April 28 and May 14, 1988, FRB73 X FRMO17; location study at Urbana April 28 and May 14, 1988, Pioneer 3377, and at Palmerston North October 28, 1987, Dekalb XL 12AA. Row width was 0.76 m. All plots were irrigated when needed except for irrigation study plots during a severe drought.

Vascular bundles develop from the procambial traces to form interconnections between mature leaves according to a precise phyllotaxis (the arrangement of leaves on a stem in relation to one another). The phyllotaxis thus affects how leaves are interconnected by vascular tissue. A shoot is said to have a 2/5 phyllotaxis if a new leaf grows in the same direction as another that is five leaves below or above it on the main stem, and if an imaginary spiral connecting the five leaves in order of production would make two turns about the stem. Spiral arrangements taken clockwise and counterclockwise are not always equal for a population of plants.[50]

In cottonwood, the denominator of the phyllotactic ratio indicates the number of major vascular bundles, or sympodia, in the stem (a sympodium can also denote a shoot that terminates in a floral bud).[43,48] During growth and development to an LPI of 16 (16 visible leaves on the main shoot), stems of cottonwood seedlings progress through 2/5, 3/8, and 5/13 orders of phyllotaxis. Each leaf always connects to three different sympodia via three leaf

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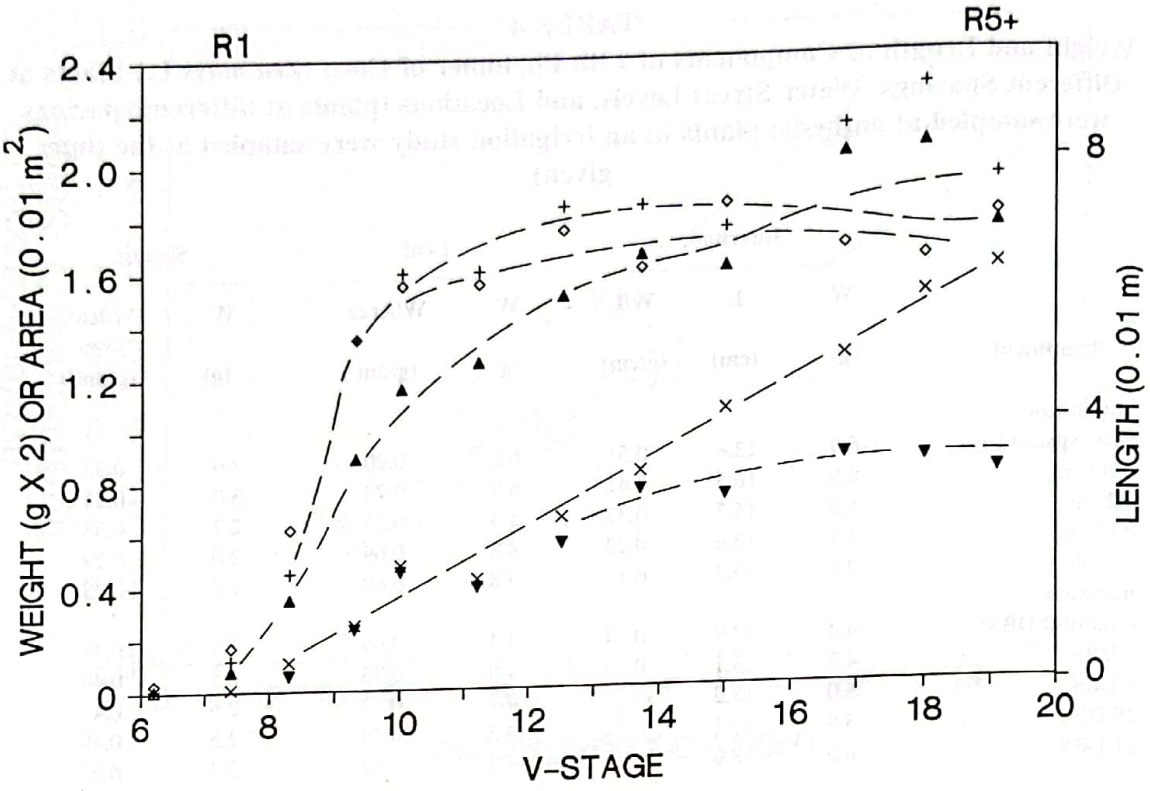

FIGURE 7. Areas, lengths, and dry weights of phytomer components of the 7th phytomer of soybean, *Glycine max* (L.) Merr. cv. BSR 201, for plants spaced every 0.05 m in the row and 0.76 cm between rows. Graph shows progress of leaf, petiole, and internode by growth stage. + = leaf area, ▲ = leaf weight, ◊ = internode length, × = internode weight, ▼ = petiol weight. R1 denotes the beginning of flowering; R5 is the stage at which pods at highest node on the main stem contain visible growing beans. (Data from Hesketh et al.[48])

traces, in a systematic manner controlled by the phyllotaxis. Each new procambial strand or differentiating vascular tissue at the tip of a sympodium is initiated and differentiated in sequence within the apical region according to its position in the phyllotactic array. These vascular strands develop long before the leaf primordia they ultimately serve appear: in cottonwood about five LPI units earlier.[43] Such activity may therefore influence where primordia develop on the apical dome, although which comes first is still controversial.[49]

Thornley[51] discussed the many theories concerning the way in which primordia are initiated in an apical dome to give a specific phyllotactic pattern. Turing[52] developed a theory for chemical control of primordia initiation based upon four assumptions: (1) a growth regulator moves according to the diffusion equation; (2) it is degraded at a rate proportional to its concentration; (3) the existing primordia synthesize the growth regulator; and (4) a new primordium may be initiated when the growth regulator drops below a certain level so that the morphogen acts as an inhibitor. Setting up and solving the appropriate diffusion and chemical kinetic equations in one dimension, with appropriate constants, can give results that mimic phyllotactic spiral behavior, including the angle at which the leaf primordium grows from the stem. Adding a spatial requirement or a packing constraint enabled the model to mimic nonspiral phyllotaxis, where no leaf is directly above any other as in a helix arrangement. Thornley[51] gave detailed examples of how such a model can be used to predict behavior of phyllotactic systems.

The placement of successive new leaves in a spiral, expressed, for example, in the phyllotactic ratios 1/3, 2/5, 3/8, and 5/13, can be described by the mathematical Fibonacci series: each numerator or denominator sums the two before. The helices with no leaves directly above one another are called parastichies and are described by the numerator of the ratio only. Larson[43,47,48] used these concepts in his analysis of cottonwood phyllotaxis; his papers are required reading for any would-be stem modeler.

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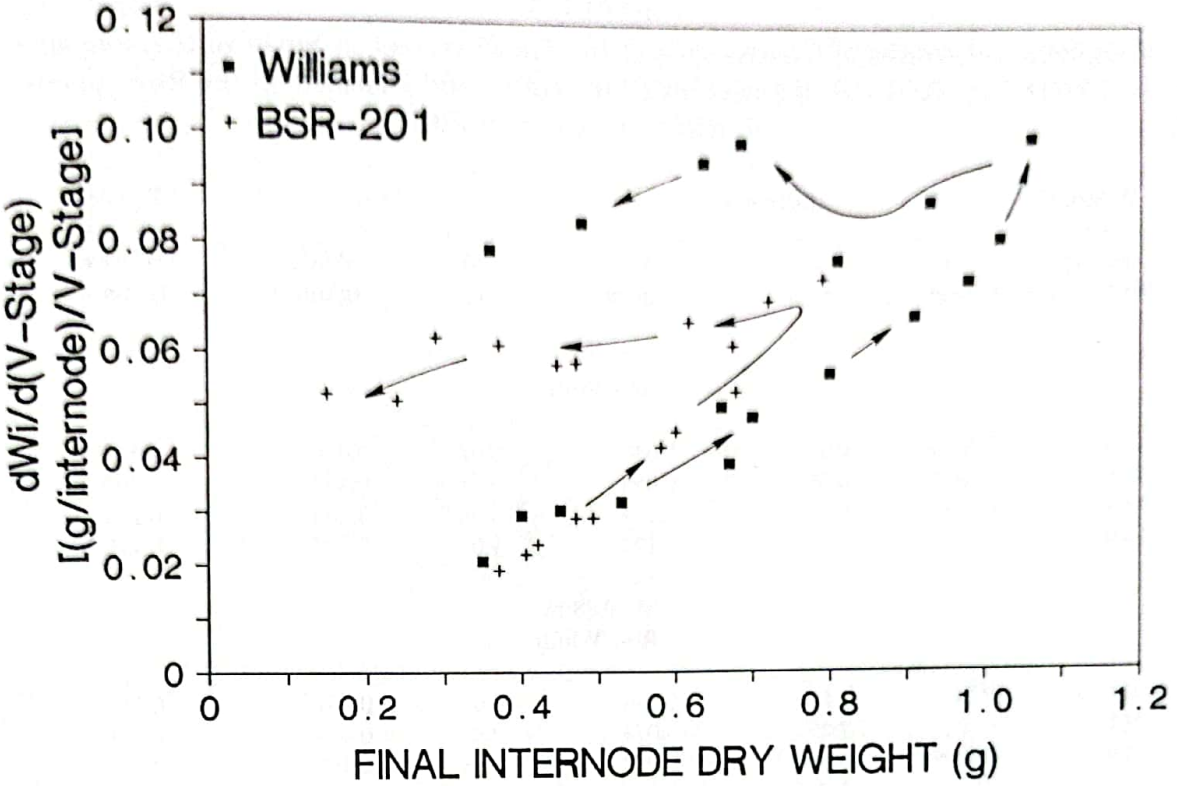

FIGURE 8. Rates of soybean internode dry matter accumulation per V-stage (regression coefficients for dry weight data for each internode as measured at different stages of growth or V-stage) plotted against the internode weight after R5, when pods were filling at the top of the plant. Here V-stage was approximated by the number of mainstem leaves longer than 0.01 m above the unifoliolates. Arrow direction denotes increasing height on the mainstem. Average R^2 values were 0.95 for an average 12 measurements, with the number of measurements decreasing with internode number. The V-stage intercepts where dry matter started to accumulate at a linear rate were usually one V-stage later than that for the phytomer.

After reaching a certain height, alfalfa (*Medicago sativa* L.) stems with alternate leaves have four bundle complexes supplying three traces of vascular tissue to each leaf.[16] The middle trace of a trifoliolate is joined to two bundle complexes on one side of the stem, with the side traces coming from the other two complexes on the opposite side of the stem. Fahn[13] published a stem sympodia-leaf trace diagram for *Chenopodium glaucum* L.; its leaves are supplied by traces from three vascular bundle systems from two of five sympodia. Lersten and Carlson[24] showed in a diagram how trifoliolates of soybean are supplied with three traces from three different sympodia (Figure 9).

Fahn[13] and Esau[12] duplicated a diagram showing how leaf traces are interconnected in a corn stalk (Figure 10). Leaf midrib and large lateral bundles first penetrate deep into the stalk before extending toward the outer parts of the stalk in lower internodes; smaller lateral bundles stay close to the outer stalk, fusing with peripheral bundles farther down the stalk. Bundles are interconnected at each node.

B. XYLEM

Predicting transport rates for nutrients, water, or growth regulators to and from an organ via the vascular system requires a knowledge of xylem and phloem anatomy. Simple theory for water flow through pipes does not apply, because of constrictions in the transport pathways mentioned. Such tissue, whose phyllotactic arrangement we have already discussed, is not made up of unobstructed tubes between organs.

Xylem tissue for water transport consists of two types of tracheary elements: tracheids (single cells) and vessel members or elements, joined end to end to form multiple cell units.[11] Tracheids are interconnected only by "pit pairs" occurring at the same point in two adjoining

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TABLE 5
Weights and Lengths of Components of the 7th Phytomer of Soybean (*Glycine max* [L.] Merr.) cv. BSR-201 at Different Row Widths and Densities in the Row (plants sampled at early pod fill)

Within row spacing ($m \times 10^{-2}$)	Internode			Leaf		Petiole
	W (g)	L (cm)	W/L (g/cm)	W (g)	W/area (g/dm^2)	W/area (g/dm^2)
			At 0.76 m Row Width			
2.5	0.38	8.35	0.046	0.62	0.416	0.193
3.2	0.46	8.35	0.055	0.71	0.433	0.204
5.1	0.67	6.52	0.102	0.96	0.466	0.203
9.7	0.57	4.45	0.127	1.03	0.483	0.175
			At 0.38 m Row Width			
4.7	0.39	8.55	0.046	0.62	0.437	0.218
6.4	0.54	7.25	0.074	0.82	0.435	0.201
9.9	0.50	6.00	0.083	0.83	0.491	0.205
11.4	0.45	3.90	0.115	0.82	0.477	0.168
S.E.	0.05	0.243	0.0071	0.043	0.012	0.009

W = mass in g, L = length in 0.01 m (cm), area = area per trifoliolate in 0.01 m^2 (dm^2). Crop was planted at Urbana, IL, May 12, 1988. BSR-201 is Maturity Group II indeterminate, which matures early at the Urbana latitude. Similar data were taken for a Group III late-maturing cultivar and two determinate cultivars of early and late maturity planted along with BSR-201.

cell walls and having a common membrane. Vessel members have perforated areas in their walls that link them to form a long vessel. The perforations, usually on ends but sometimes also on side walls, constitute a perforation plate that may have one or many openings. Vessels can be 1 to 5 m long or may extend through an entire mature tree. Water with its dissolved substances may flow through thousands of thin pit membranes in tracheids and perforations in vessels before reaching a leaf.

Secondary xylem, created by the cambium, is wood. Here, xylem cells are arranged in both a vertical system and a transverse system, with pit or perforated interconnections. The vertical system consists of nonliving tracheary elements, fibers for support, and living parenchyma cells. The transverse system consists of ray cells, which are living parenchyma. They connect with living cells of the vertical system. A continuum of living cells thus penetrates the wood and is often connected via the ray cells with living cells of the pith, phloem, and cortex.[11]

C. PHLOEM

Phloem for transport of organic materials is made of sieve elements. These can consist of either sieve cells interconnected by sieve areas or, as in most monocots and dicots, of sieve-tube members or elements, groups of cells interconnected with sieve plates. Sieve elements generally are 20 to 40 µm across and 100 to 500 µm long, with pores 0.1 to 5 µm wide in interconnecting sieve areas or plates.[53] Sieve elements lose the cell nucleus upon maturing.

Some cytoplasm (very undifferentiated protoplasm) remains in sieve-tube elements and can sometimes be seen in the pores, along with other materials. Researchers disagree about whether such pores are open or contain filaments; results may be artifacts of methods used to prepare material for microscopic observation. Weatherly[54] discussed the effect of small pores

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TABLE 6
Nodes per Plant and Weight per Ground Area for Soybean (*Glycine max* [L.] Merr.) cv. BSR-201 at Different Row Widths and Densities

Within row spacing (0.01 m)	Mainstem nodes per plant	Branch nodes		Weight per unit ground area (g/m²)			
		Per plant	Per m²	Stems	Branches	Leaves + petioles	Total
			At 0.76 m Row Width				
2.5	13.4[a]	6.0	745	230	22	291	543
3.2	15.1	7.0	633	226	30	310	555
5.1	17.5	15.2	708	240	42	385	667
9.7	18.8	36.0	661	129	58	301	487
			At 0.38 m Row Width				
4.7	13.4	2.6	615	251	11	258	520
6.4	16.4	5.3	673	263	25	370	658
9.9	16.8	16.9	740	176	41	277	494
11.4	18.9	40.5	752	123	77	321	521
S.E.	0.51	1.38	41	28	6.4	44	

[a] Interplant competition has always resulted in fewer mainstem nodes in our experiments.

containing cytoplasmic filaments on a Munch-type mass flow model for organic matter transport in phloem sieve tubes. He concluded that such a hypothesis is compatible with the existence of filaments 100 to 200 nm apart in the sieve pores. He also presented other evidence for and against such a hypothesis.

There are many hypotheses implicating the residual cytoplasm of sieve-tube elements in active transport processes, which greatly complicate our understanding of phloem transport. Other phloem components that play a role in models are the companion cells, specialized parenchyma cells common in phloem of monocots and dicots, that originate with an associated sieve-tube member but retain their nucleus. Companion cells play a role in most models for loading and unloading organic materials carried in sieve tubes.

There is a vast amount of quantitative information about movement of materials in stems, information that is independent of any consideration of the anatomical structures involved. Mass flow with open pores in the sieve plates easily accounts for the flow rates observed whereas other hypotheses do not. Books edited by Aronoff et al. (see Weatherly[54] and Wardlaw and Passiouri[55]) contain extensive analyses of such problems both in papers and associated discussions. Moorby[56] recently reviewed the status of phloem transport models.

VI. AXILLARY BUDS AND BRANCHES, MODIFIED STEMS, AND ADVENTITIOUS BUDS

Buds are stems with short internodes.[1] Terminal and axillary (lateral) buds, able to produce shoots or floral structures, arise directly from the apical meristem. Branches and modified stems such as tillers, stolons, rhizomes, corms, and tubers originate as axillary buds. Adventitious buds, which arise distant from the apex, can produce roots.

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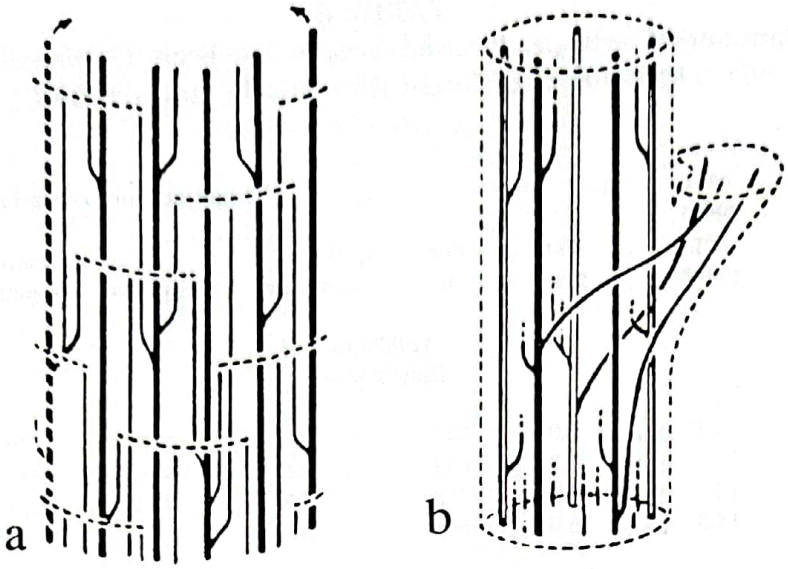

FIGURE 9. Vascular pattern in stem of soybean, *Glycine max* (L.) Merr. In diagram A, fine traces that stop entirely at a broken line represent vascular tissue entering a petiole; this is shown more clearly in diagram B. Each of the three fine traces come from a different main trace or sympodium, of which five are shown. This supply system means that parts of different leaves up the main shoot are closely interconnected. (From Lertsten, N. R. and Carlson, J. B., in *Soybeans: Improvement, Production, and Uses*, Wilcox, J. R., Ed., American Society of Agronomy, Madison, WI, 1987, 49. With permission.)

A. AXILLARY BUDS AND BRANCHES

Axillary buds are frequently initiated when the LPI is two.[11] These buds appear to originate in the axils of leaf primordia but are really in interfoliar positions.[29] They arise from undifferentiated cells from the apical meristem that are displaced down the stem as "detached meristems" or from partly differentiated cells, usually parenchyma, of the internode. Further development of axillary buds is inhibited when they are near the apex and frequently when they are lower on the mainstem. This suggests that growth regulators transported down from the apical meristem in vascular tissue inhibit the growth of other meristems (see section, "The Role of Plant Growth Regulators"). Axillary buds at some distance from the mainshoot apex can develop into shoots, especially if the mainshoot apex is pruned from the plant.

Many physiological studies have been conducted on the initiation and development of both axillary and adventitious buds. Both plant growth regulators and the nutritional status of the plant are involved, along with temperature and daylength.

Shoot phytomers import or export materials to and from the rest of the plant and thereby contribute to the growth of the rest of the plant.[57] Location, ontogeny, and physiological activity of each phytomer on the plant are all important in any simulation of plant growth with a model. Figures 3 to 6 and Tables 1 and 2 summarize some of the types of information needed.

When measuring the thermal time between successive phytomer events, one must distinguish between vegetative and reproductive growth. If the main or branch shoot maintains a vegetative apex, with any floral buds occurring at lateral positions, the shoot system is sometimes called a monopodium. Examples are main shoots and their lower-node branches in many plants and most stolons. In the reproductive state, this vegetative apex can be replaced by a reproductive one through the reorganization of multiple modified phytomers;[11] this occurs in both gymnosperms such as conifers and in flowering plants. Once the shoot terminates in a floral bud (a shoot system sometimes called a sympodium), new vegetative phytomers can develop from axillary buds. The timing of growth in this case depends upon how fast each successive axillary bud develops into a new phytomer.

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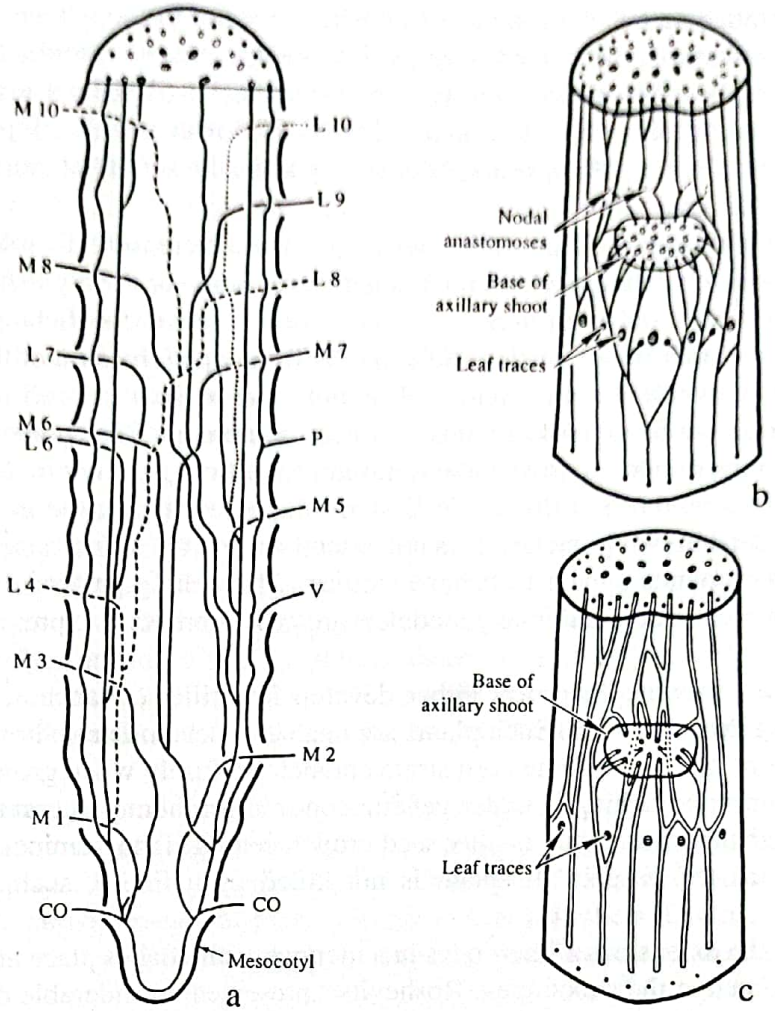

FIGURE 10. Vascular pattern in stalk of corn, *Zea mays* L. Diagram A of stem with 10 nodes shows median or midrib (m), lateral (l), coleoptile (co) and vestigial (v) traces. Diagrams b and c show the inner (b) and outer (c) vascular connections between the main stalk and axillary shoots (vegetative branches, ears), indicating how the vascular traces interconnect. (From Esau, K., *Vascular Differentiation in Plants*, Holt, Rinehart & Winston, New York, 1965. With permission.)

Reproductive branches of cotton (*G. hirsutum* L.) are made up of a succession of sympodia;[25] each consists of one phytomer terminating in a floral bud, with buds in the axil of the leaf capable of forming new sympodia. The time between new leaves or reproductive events within a reproductive branch is more than twice as long as the time between new leaves or events at comparable positions on successive branches or between leaves on a vegetative branch off the main stem.

In cotton, the vegetative meristems of monopodia rarely abort but do become inactive when the plant is loaded with growing bolls. The mainshoot terminates with the first flower on a tomato plant (*Lycopersicon esculentum* L.) and on many related Solanaceae (nightshade family) weed and crop plants: pepper (*Capsicum annuum* L.), potato (*Solanum tuberosum* L.), eggplant (*S. melongena* L.), bitter nightshade (*S. dulcamara* L.), Eastern black nightshade (*S. ptycanthum* Dun.), and jimsom weed (*Datura stramonium* L.). What seems to be further mainstem growth or dichotomous branching is really growth from axillary buds at phytomer nodes below the flower. Each successive flower or cluster of flowers at what appears to be a mainstem or dichotomous branch node is a terminal fruiting organ.

Detailed descriptions of such growth in the tomato[2] and potato[35] serve as good examples

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for sympodial branching behavior in other nightshade species (although we found that tomato plants did not necessarily behave exactly as described in the literature). In a potato plant, sympodia frequently develop from the two mainstem leaf axils below a flower stalk. The higher sympodium develops 5 to 12 leaves whereas the lower one develops 11 to 17 leaves before the terminal flower stalk appears,[35] depending upon the genotype, position on the plant, and growing conditions.

Jimsomweed and pepper plants exhibit what appears to be regular dichotomous branching behavior, with one vegetative phytomer and one flower. Some of the nightshade weed species also exhibit this type of behavior under some conditions. Vegetative dichotomous branching occurs in lower vascular plants, such as Selaginella, from equal division of the original apical meristem into two vegetative meristems.[11] It is not clear to us how such regular branching behavior can originate from axillary buds on lower phytomers. Two branches appear at the same time from lower nodes, to give under optimum conditions 2n phytomers (2, 4, 8, 16, etc.) for each node n above the first flower. In Eastern black nightshade, the internode on one of the regularly occurring two branches does not extend, giving the appearance of a monopodial mainstem. Tomato plants appear to behave similarly. Branching patterns in the Solanaceae deserve study in greater detail, as many modelers are now attempting to predict growth in such species.

Axillary buds on corn phytomers either develop into tillers, branches, or ears or abort sometime during kernel growth. Such plants are unable to develop new shoots after maturing seed and therefore die. Since some corn strains branch profusely when grown by themselves while others do not, branching is under genetic control. Sorghum plants retain the ability to develop new branch shoots or tillers after seed growth ceases in the terminal head of the main shoot. As long as the base of the plant is not killed by a freeze, such plants can grow indefinitely.

Shooting, or the extension of internodes in a monocot culm, takes place after the reproductive head is initiated at the shoot apex. Roshevits[64] presented considerable detail about these structures in grasses. Thomas[30] used the phytomer concept to discuss anatomy of a stolon in a legume, white clover (*T. repens* L.). It is monopodial in behavior, with new shoots arising from axillary branches at nodal positions on the stolon and new roots arising from adventitious buds.

Development of axillary and adventitious buds of a phytomer unit, together with monopodial and sympodial behavior, thus results in complex branching behavior as well as a source of new roots. The tomato plant serves as a good example for branching behavior in many of the Solanaceae plants. However, as one begins to compare more and more species, as Roshevits[64] did (see following section) for the grasses, single didactic examples become less and less useful.

B. TILLERS, STOLONS, RHIZOMES, AND TUBERS

Roshevits[64] reviewed in detail the anatomy and branching behavior of grass culms (stems), with comparisons among species. A tiller is a branch of one of a number of closely spaced nodes (short internodes) at the basal part of the culm. These tillering nodes are usually below ground but not always, as in rye (*Secale cereale* L.), for example. Nodes at the base of the tiller have axillary buds that can produce new tillers and adventitious buds producing roots.

If the axillary branch remains within the leaf sheath before emerging, it is called an intravaginal shoot. If it pierces the sheath, it is referred to as extravaginal. Extravaginal shoots grow horizontally at first. Intravaginal shoots grow upward but can grow horizontally and become stolons, or stems that root at nodes, as do many grasses and plants, such as strawberry (*Fragaria* spp.) (see Figure 1). Stolons produce well-developed leaves at nodes; stoloniferous nodes that touch the soil surface produce adventitious roots and axillary shoots. Such intravaginal branching results in dense clumps, while extravaginal branching does not. Both can occur in some species, such as bermudagrass (*Cynodon dactylon* [L.] Pers.).[22]

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While tillers are intravaginal shoots, rhizomes are horizontal stems that are almost always extravaginal. Usually fleshy and underground, rhizomes are important storage as well as reproductive organs common among monocots, such as grasses and *Iris* spp. (Figure 1). They form at a tillering node. Green leaf blades do not develop on underground rhizomes; leaf sheaths do, but soon wither away. Buds may develop in the axils of the leaf sheaths and may form new rhizomes or a shoot. The apical meristem of the underground rhizome may produce a new shoot with new rhizomes when it penetrates the soil surface, exhibiting sympodial branching behavior, or it may stay underground with shoots arising from axillary buds, exhibiting monopodial branching behavior.

Underground rhizomes produce adventitious roots at each node. The lower internodes of the culm and the rhizome can store carbohydrates, contributing to the perennial behavior of some grasses. If storage substances accumulate in one basal internode, it assumes a globular shape; if accumulation occurs in several, the basal part of the culm assumes a beaded shape made up of a succession of globules.

Roshevits[64] compared axillary growth among many grass species; he found transitions between branching, tillering, stoloniferous, and rhizomatous behavior. Horizontal extravaginal branches along the soil surface readily put down adventitious roots at nodes and continue to branch profusely, forming a mat of plants. Since such growth is not intravaginal, it is stoloniferous. Roshevits,[64] Williams,[65] and Simmons[70] discussed the effects and interactions of plant age, environment, and cultivar or species on the different kinds of axillary stem growth discussed here.

Tubers and corms, as modified stems with short internodes, are important storage organs for some herbaceous dicots (Figure 1). Tubers, mostly underground, bear buds from which new plants can sprout. Milthorpe and Moorby[72] discussed timing and factors governing the initiation, growth, and dormancy of potato (*S. tuberosum* L.) tubers. Corms, or short bulbous underground stems as in Gladious spp., bear roots and can bear vegetative propagules.

C. ADVENTITIOUS BUDS AND ROOTS

Buds that originate independent of a mainshoot or branch apical meristem are called adventitious. Such buds, which can give rise to adventitious roots, can develop on stems, roots, or leaves of intact plants or on cuttings. They are common on stems of monocots and on rhizomes.

Roots can develop from adventitious buds just above the node on internodes in grasses such as corn.[58,59] Nodes with root development can be on or in soil (crown nodes) or can be anywhere on the shoot. Such roots readily develop on sugarcane (*Saccharum* spp.) stem pieces or on grass stems that grow near the soil. New shoots can develop from adventitious buds on roots. Adventitious buds usually dedifferentiate from parenchymous cells near the stem surface but also can originate in deep-seated tissues within the stem. Most of the grass root system originates from such buds. The dedifferentiation process that parenchymous cells undergo in order to become meristematic is in need of research. Figure 11 (Zur et al.[58] showed a similar figure using a different set of data) compares the effect of degree days on production of adventitious roots in relation to other organs in corn stalks.*

* See Kiniry et al. (Chapter 5) for a review of the status of temperature response or degree day models for predicting leaf developmental events needed to relate growth stages, such as shown in Figures 5 to 8, to real time. Figure 11 does not represent a valid test for the model used, but because of the errors involved in temperature and event measurements, and the difficulties in quantifying the effects of stresses or growth stage on event rates, our analysis involving four kinds of events measured by the same person in three diverse field environments may represent the state of the art, but see Wang et al.[79] Researchers now are hoping to quantify nonlinear responses with both simple models and more complex ones, using temperature means during short sampling periods. The model we use and similar models tested by others indicate the general nature of what may be the nonlinear temperature response; such responses have been measured for corn in controlled environments.[59,80,81] The emphasis now is on obtaining data on plants growing in cool maritime climates where mean temperatures near the threshold for growth prevail. The quest for a better degree day model for predicting developmental events has been a long one; the problems we are encountering are not new.

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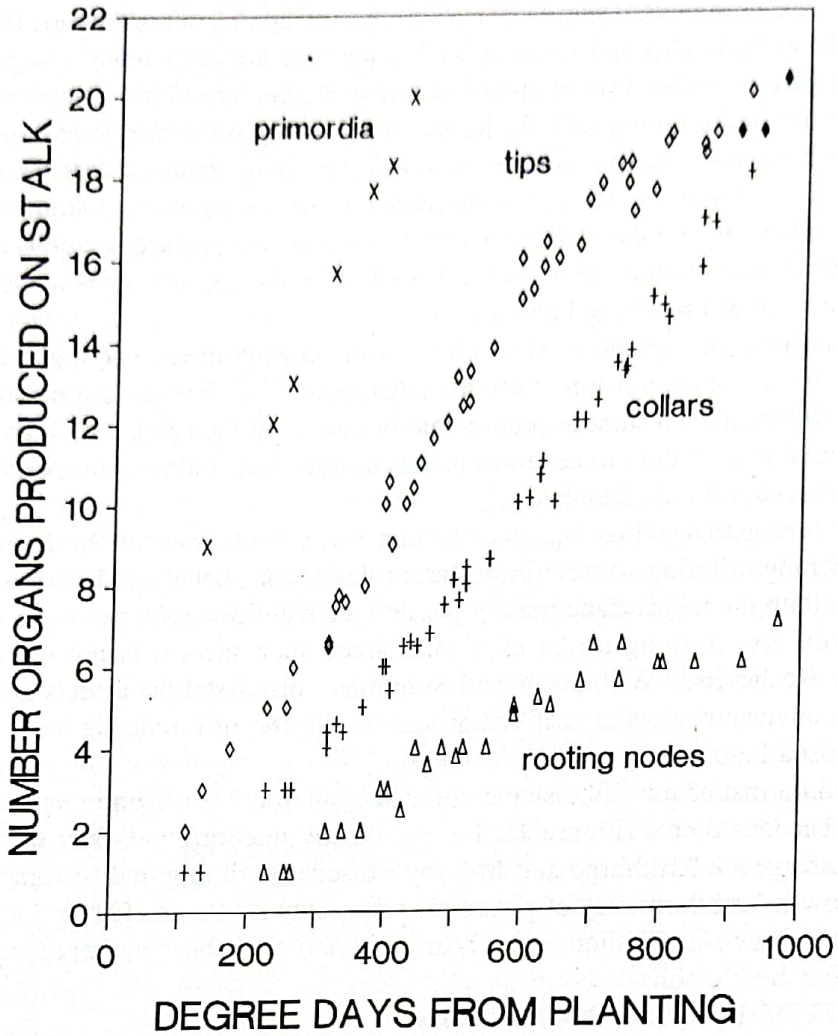

FIGURE 11. The effect of degree days on production of adventitious roots at lower stalk nodes of corn, compared with production of leaf primordia, tips, and collars. These data were for three very different growing seasons at Palmerston North, New Zealand and at Urbana, IL (1987 and 1988). The base temperature for the degree day calculation was 6°C, with the difference between the maximum temperature (T_{max}) and 30°C subtracted from the calculation when T_{max} was greater than 30. See text for a discussion of why such a model was used. (Adapted from Zur et al.[58])

VII. THE ROLE OF PLANT GROWTH REGULATORS

We previously discussed the effects of gibberellins on internode extension in dwarf plants. Wareing and Phillips[60] presented a good review of how plant growth regulators are thought to control axillary meristem growth or branch development. Trewavis and Allan[57] challenged some of the current dogma after analyzing the kinds of experimental systems, techniques, and results involved.

Many studies link increased far-red levels in shade with increased internode elongation. Ballare et al.[66] demonstrated that mirrors reflecting far-red light onto the plant resulted in longer internodes in *Chenopodium album* L. (common lambsquarter) and *Sinapsis alba* L. (mustard). They suggested that the red to far-red ratio of light in a plant stand serves as an early warning of impending competition. Begonia and Aldrich[61] showed that light passing through broadband acetate filters reduced the production of fruiting branches in soybean. Based on measurements of endogenous growth regulators in shoot apices and axillary meristems, they suggested that shade with a low red to far-red ratio induced higher levels of indole-3-acetic

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acid in shoot apices and internodes; this induced abscissic acid synthesis in the axillary meristems, which suppressed growth of such meristems. Such results support the prevailing dogma.

Trewavis and Allan[57] challenged assumptions about where such endogenous growth regulators are synthesized. They suggested that a chemical that binds these regulators as they flow past through the vascular system might be synthesized at sites where the regulators are found; these researchers also worried about interactions with the supply and demand of nutrients. The associated controversy is reflected in a review of what is known about binding sites.[62] Our concern here is how to research and quantify interactions of plant growth regulators with nutrient supply and demand in order to achieve an integrated approach for studying such phenomena.

In photosynthetically competent mustard plants, irradiation of the first internode with supplementary far-red light caused a rapid increase in extension growth.[67] The increase in extension rate depended on the amount of light applied. Red light reduced the extension rate. The extension effect is short-lived once the supplementary light is switched off. Casal and Smith[68] showed a long-term effect of such treatments in mustard seedlings, sensed by leaves rather than internodes and requiring a different set of treatments. They reviewed the status of related research, analyzing the phytochrome system involved and discussing ecological implications.

VIII. BRANCHING PATTERNS

To paraphrase Watson and Casper,[33] plant growth results from the continual production of phytomers by meristems. An aggregate of successive phytomers produced by the same meristem, whether at the main shoot apex or on a lateral branch, is called a module. An aggregate of successive phytomers, connected by vascular tissue, which generates its own supply of photosynthate, is called a "semiautonomous integrated physiological unit". Flowers and inflorescences develop through production of successive phytomers bearing modified leaves.

Plants develop flowers either on the main shoot apex or on axillary branches, resulting in determinate (sympodial) or indeterminate (monopodial) growth, as was discussed in detail under "Axillary Buds and Branches". Axillary branches, as in the case of the tomato plant, can appear as a continuation of the mainstem, with the terminal flower stalk appearing to come directly out of the stem. If such branches continue to develop, the tomato plant can appear to be indeterminate. If instead, the main shoot apical meristem aborts or becomes irreversibly dormant, as in the case of an indeterminate variety of soybean during late podfill, the plant can appear to be determinate. Dichotomous sympodial branching in some Solanaceae (nightshade) plants can result in a single stem if the internode of one of the branches does not extend, and further development in that branch is suppressed.

This discussion shows that while morphogenic definitions do not always predict a specific pattern of shoot development, they do indicate rates of leaf appearance on a branch or on what appears to be the main shoot. The definitions can indicate rates because of the extra thermal requirement for growth and development of an axillary meristem over that of a new phytomer on a monopodial shoot. Shoot extension depending upon development of an axillary bud can be slowed while the bud resumes growth.

For example, in the case of a cotton sympodium, only one leaf is produced, and new leaves develop on new axillary phytomers at a uniform rate. In the case of the tomato or potato, 3 to 17 leaves may develop within a sympodial branch, as described in the literature (our tomato plants did not always stay within this range); leaves may appear rapidly, with a pause while a new axillary bud begins to form a new sympodium.

In the tomato, the leaf initiated below the terminal flower stalk joins with the axillary

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sympodium and ends up displaced above the flower stalk which then appears to come directly out of what seems to be the main stem. The tomato flower is supplied with photosynthate by the two subtending leaves, but the fruit is supplied by these two leaves and the one just above.[63] Since the vascular network linking leaf and fruit is determined by where the leaf originated, such morphological detail can help explain physiological behavior and should be worked out as soon as possible.

In the soybean population study associated with Tables 5 and 6, the early-maturing indeterminate plant never produced an axillary branch with a conspicuous leaf above the fifth node. An early-maturing determinate line branched similarly up to node 5 but produced multiple branches with short internodes and small leaves for nodes 6 through 10. The late-maturing indeterminate line (group III vs. group II) produced major branches up to node 6 and minor branches such as those at the higher nodes of the determinate line at nodes 10 through 13. These minor branches sometimes occurred in pairs up to node 17 in plants 30 cm apart at the 76 cm row width. The late-maturing determinate line produced the same number of mainstem nodes as the early determinate line but branched more. Thus, the four locally grown cultivars tested exhibited four kinds of branching behavior.

Determinate group VII lines that did not flower under the mid-season long days at Urbana, IL, could be induced to flower by lengthening the dark period. If the longer dark period was eliminated at flowering, such lines went through cycles of producing multiple, short, flowering branches at various mainstem nodes without setting pods. In this case, vegetative axillary buds were able to develop a few phytomers before ending in a flower, producing clusters of branches from the same node.

Stulpnagel[69] presented a coded list of different kinds of branching found in cultivars of *Vicia faba* L. (broadbean). Such a list is needed for modeling purposes for many other cultivated and weed plants.

IX. COMPLICATIONS OF GENETIC AND ENVIRONMENTAL RESPONSES

This presentation tends to somewhat oversimplify the problem of understanding branching behavior and patterns. For example, widely spaced soybean plants have shorter internodes than plants in a standard planting, and their branches are well developed. Soybean seedlings pruned by animals will rapidly develop axillary branches from the lower nodes. The amount of branching in a given condition is under genetic control. Some corn strains tiller and branch profusely if spaced wide apart in cool climates; some cotton races branch more than others growing under the same conditions.

In CO_2-enriched environments sunflower plants, which normally do not branch, can readily convert excess photosynthate into new stem tissue at 20°C, with little buildup of leaf starch; under these conditions certain plants of other species do not accumulate starch. Soybean plants at the right stage of growth can branch profusely, with secondary and tertiary branches. In cool maritime climates at ambient atmospheric CO_2 concentrations, normally spaced corn plants can develop unusually heavy internodes. Such abnormal stem or branch behavior determines how these species might be expected to respond to an increase in global atmospheric CO_2, excluding C_4-C_3 effects on photosynthesis response.

Plants self-thin at high population densities or under water or pest stress, with "aggressive" plants as large as or larger than average plants at low population densities. Aggressive plants branch and compensate for weak plants that have succumbed to stress. In seemingly uniform stands of soybean infected with root and stem rot, diseased plants are hidden by the branches of healthy plants, and apparent uniformity masks considerable plant- to-plant variability. Aggressive plants in severely droughted corn stands are conspicuous and can grow large ears.

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X. EXPERIMENTAL PROTOCOL

Our discussion suggests the experiments needed to study stem growth and development. The growth of axillary or adventitious buds depends upon the supply of nutrients, timing of the supply relative to bud growth and development, and the growth regulator status. Stand density is a major factor controlling nutrient supply. Temperature controls the nutrient demand in growing organs, while complex environmental and physiological factors control the number of growing organs.

Supply and demand can be manipulated as follows, using standard research techniques, to study mainshoot and branch growth and development.

1. Pruning experiments: prune the shoot apex and study axillary bud growth and development.
2. Photosynthetic supply experiments: use shades, CO_2 enrichment of the air, temperature, leaf pruning, supplementary lights, and plant spacing to manipulate photosynthetic supply.
3. Photosynthetic demand experiments: prune growing reproductive organs, manipulate temperature, prune leaves.
4. Mineral nutrient supply and demand experiments: use a hydroponic culture to withhold or reinstate nutrients abruptly; use standard field or controlled-environment experimental techniques to control supply.
5. Water stress and irrigation experiments: conduct under natural conditions or in rain-protected plots.

Detailed weather data should be compiled in these experiments. For light, continuous records or short-term integrated flux rates are preferred. Rainfall needs to be measured near the experimental plots. Different planting dates and locations at different elevations or latitudes can be used to vary temperature and photoperiod.

As in any other research, such an effort would be exploratory and might not lead to any worthwhile discoveries. However, it can be done using traditional field plot techniques, with a dissecting microscope and some knowledge of plant anatomy and phenology. Plotting physiological measurements against growth stage seems to help transcend the limitations of location effects in field research by standardizing the time scale. Developing a whole-plant seasonal synthesis in this way may lead us to essential new information about how plants grow and yield.

XI. SOME NOVEL MODELING PHILOSOPHY

This review emphasizes the experimental and theoretical aspects of developing a logic to quantify the ways in which plants grow and yield. Few models account for the morphological aspects of growth and development we have described; most plant growth models are empirical. Yet much can be learned about plant growth by developing detailed (organ by organ), mechanistic, nutritionally based models, as suggested.

Despite all the systems analysis philosophy that modelers subscribe to, few modelers with little time for research ever detect the factors controlling the system they try to simulate or study. The systems we describe must be observed first hand for long periods before one can detect the controlling factors. One needs to screen out all the traditional and sophisticated logic and techniques available for field research and continually ask oneself: What unknown factor is limiting this experimental system? Is the research approach irrelevant?

For example, in the Midwest, as typified by the experimental site at Urbana, IL, overriding factors in the soybean production system under study were root and stem pests and their

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interactions with water stress. The soybean population in the study associated with Tables 5 and 6 had to be irrigated at planting; excessive frequent irrigations led to root and stem diseased plants (mainly phytophthora root and stem rot [*Phytophthora megasperma* f. sp. *glycinea*]) that were not obvious until late in the experiment. It has been extremely difficult to quantify or predict how prevalent such diseases are or what their effect is on yield. From a distance, infected stands looked healthy and uniform.

Other important factors controlling yields in soybean production systems are lodging after a windstorm, pod shattering, and killing frosts. The severity of each factor within a field, the processes involved and the interactions with stage of growth are as difficult to quantify as a disease infection.

To cite another example: a critical factor in a water stress study during vegetative growth of a corn crop was that nodal roots at the base of the stalk were unable to penetrate the dry, hard soil surface. A second factor was that some plants in a severely stressed field dominated others and obtained adequate water for near-normal growth. After many years of studying water stress in the field, we have concluded that the best measure of stress is made through visual inspection for rolled leaves in corn or wilted leaves in other crops. Stress is much easier to see than it is to measure.

The corn and soybean phytomer experiments described and the experimental protocol given indicate the research approach that is urgently needed to develop a synthesis of information about how plant phytomers develop and grow. Given data of the kind we present in Figures 5 and 6 and Tables 4 to 6, plus estimates of growth and maintenance respiration for phytomer components or reproductive organs, estimates of the losses and accumulation of mineral nutrients, a thermal model to predict growth stage and process rates, and similar information about root growth, one can begin to synthesize a nutritional budget, including one for water, for a plant. From such a synthesis, one can hope to learn how nutrients are partitioned in plants and how plants might respond to an increase in CO_2 in the global atmosphere. One might also learn how to breed better plants, to manage better crops, and to forecast yields more accurately.

We emphasize that the subject matter discussed in this review is a limiting factor for development of credible plant growth and yield models. Some of the best sources reviewed here are quite old,[15,64] suggesting that we need to consider some of the earlier literature before proceeding much further with new research. Agricultural research is divided into disciplines relevant to the overall problem, yet there is no organized discipline related to plant morphogenesis. Perhaps this book is a beginning.

ADDENDUM

We should have included additional sources[82-84] for crop morphology, which were helpful to us in a further analysis of how morphology controls phenology. We also recently located better definitions and illustrated examples of vegetative storage organs,[84-86] with appropriate literature citations for function.[86] A synthesis from these and additional sources is in press.[87] While we have made considerable progress in locating this information from many diverse botanical disciplines, experts in morphology should produce a more botanically correct synthesis soon. Educators are eager to include such information in undergraduate and graduate courses.

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Chapter 7

TILLERING IN WHEAT

R. W. Rickman and E. L. Klepper

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I. INTRODUCTION AND OVERVIEW

Tillering in wheat, or phenological development generally, can be most easily described if three basic characteristics of the wheat plant are understood. First, each leaf, tiller, and root on a wheat plant is unique and can be individually identified or named. Second, each of these unique parts appears or is developed in a precisely predefined sequence. Third, the development or appearance of these parts is linearly related to the temperature at which the plant is growing within the range of 0 to 30 or 35°C.

The objectives of this chapter are to present these three basic characteristics, show how together they provide a very simple yet extremely detailed description of plant development from which phenology can be determined, and provide the algorithms needed to determine developmental stage and phenology from daily air temperatures.

II. PLANT PART IDENTIFICATION

The method used to identify each plant part uniquely appeared in the literature from two independent sources.[1,2] It is an extension of the leaf and tiller identification used by Jewiss[3] and the development stage system proposed by Haun.[4] To quote from Klepper et al.,[1]

> "Leaves are numbered acropetally beginning with the first foliar leaf (L1). Tillers borne on the main stem bear the number of the leaf that subtends them; thus T1 is produced from the bud in the axil of L1. The coleoptile is designated as L0; the coleoptilar tiller T0. ... tillers on the main stem have designations comprising the letter 'T' and a single digit such as T0, T1, T2, etc.
>
> "Each main stem tiller can produce subtillers from buds in the axils on the tiller, including the bud in the axil of the prophyll at the base of the tiller. The leaves on tillers and the subtillers associated with these leaves bear two-digit numbers. For example, the first leaf of T1 is L11 and the tiller in the axil of L11 is T11. The second leaf of T1 is L12, and the tiller associated with it is T12. Tillers arising from the axil of the prophyll have a zero as the second digit.
>
> "In like manner, the subtillers can occasionally produce third order tillers ... which bear three digit numbers. For example T101 comes from the axil of the prophyll of T1".

III. IDENTIFICATION GUIDES AND PATTERNS

Learning that each part of a wheat plant is unique is relatively easy. Developing the ability to identify each leaf and tiller on a plant correctly requires practice and a knowledge of some common morphological features of the plant. The following features have proven helpful in providing consistent, accurate identification.[5]

The plant produces its mainstem leaves to form an overall shape similar to that of a hand-held fan. The latest fully expanded leaf is normally the longest and can be used to find the mainstem. Newest leaves appear at the center of the fan immediately adjacent to the longest leaf and fall to the left or right depending on whether they are odd or even numbered leaves. All odd numbered leaves accumulate on one side, all even numbered ones accumulate on the other. The number of fully expanded leaves plus a fraction representing the length of the newest expanding leaf relative to the length of its immediate precursor is the Haun stage of the plant.[4] The plant in Figure 1, for example, has a Haun stage of about 4.4.

Leaf L1 and the point of seed attachment, the scutellum, are reliable markers for determining the odd and even side of a plant. Leaf L1 has a rounded or blunt tip which contrasts with the very pointed tip of every other leaf on a plant. It will be the first or lowest leaf on the odd side. The zero tiller T0 or its bud will be found immediately above the scutellum. It reliably marks the even side of the plant. Positive identification of either L1 or T0 provides the orientation from which all other parts can be identified.

The tillers, excluding T0, often will be found in groups of three on plants older than jointing. Tiller T1 and its first two subtillers T10 and T11 frequently form such a group. Other common groups can be T20 and T21 with T2 and T3 and T4 with the mainstem. Tiller T0 is easily

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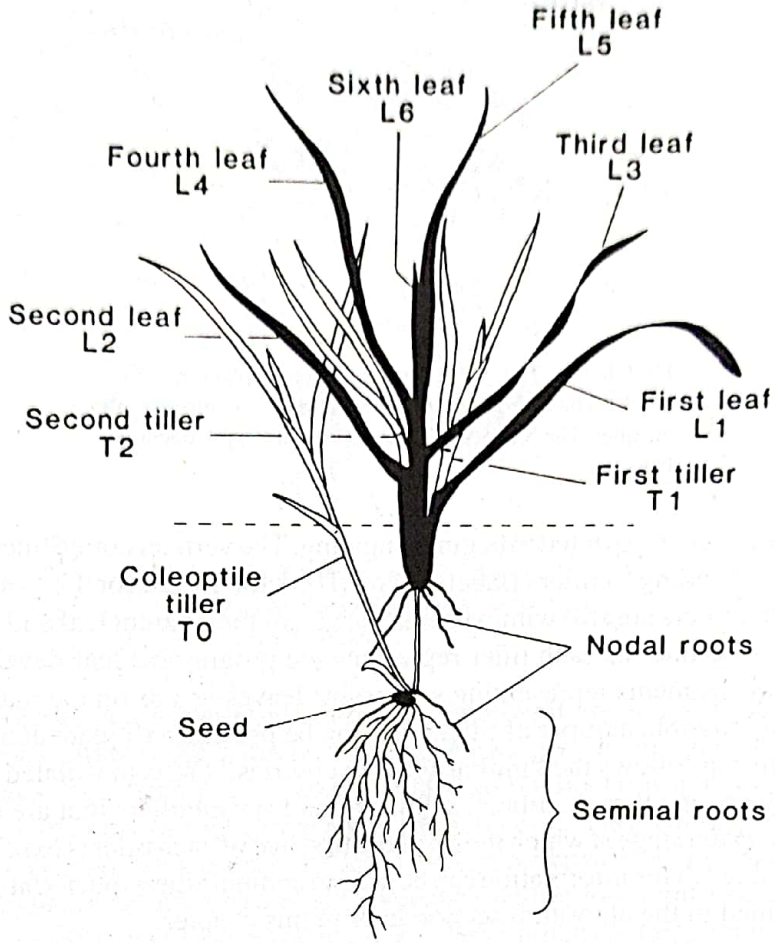

FIGURE 1. Wheat plant with identified parts.

identified when the coleoptilar or zero internode elongates as is shown in Figure 1. For shallow plantings where the zero internode does not elongate, accurate identification can be time consuming.

IV. PLANT BUILDING BLOCK STRUCTURE

Each culm, the main stem or any tiller, is created by the plant by stacking a series of identical vegetative building blocks, one upon the other. This universal vegetative building block unit is composed of a node and its associated leaf, tiller bud, roots, and internode as illustrated in Figure 2. The root labels A, B, X, Y in Figure 2 indicate the quadrant of the stem cross section in which the root forms. The timing of root appearance in the quadrants is described by Klepper et al.[6] Each culm assembles itself by creating successive blocks, one upon the other, alternating the position of every other block by 180° as shown in Figure 3.

V. DEVELOPMENT PATTERN

The appearance of plant parts follows a rigidly predefined sequence. The diagram in Figure 4 illustrates that sequence. The segmented vertical line in the center, labeled MS, represents the main stem of the plant, with each numbered line segment representing the successive leaves on the mainstem. Progression of time corresponds to upward movement along this line. The horizontal dashed lines mark the mainstem leaf development stage (Haun stage) at which the

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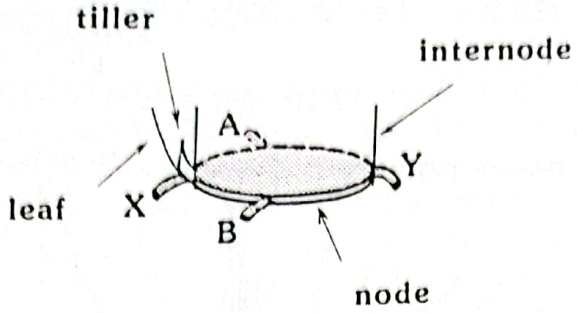

FIGURE 2. The vegetative node unit (plant building block). The A and B roots appear as a pair in unison with the tiller. The X and Y roots appear about $1^1/_2$ phyllochrons later.

corresponding tiller bud is expected to begin elongating. The vertical dotted lines beginning each vertical line corresponding to tillers (labeled 0 for T0, 1 for T1, 20 for T20, etc.) represent the time that the young tillers are still within the leaf sheath of their parent leaf and therefore are not yet visible. The solid line for each tiller represents the progressive leaf development of each tiller, with the line segments representing successive leaves just as on the mainstem.

The maximum possible number of tillers that can be present on a plant at a particular Haun stage of the mainstem follows the familiar Fibonacci series.[7] Only an isolated plant in an ideal environment will set on all of the tillers, subtillers, and subsubtillers that are possible.

The mainstem Haun stage at which the tip of the first leaf of each tiller is expected to be visible is contained in Table 1. This information can be used to compute the expected appearance of each tiller as is explained in the algorithm section later in this chapter.

VI. TIMING OF DEVELOPMENT

The time of appearance of successive leaves on the mainstem or tillers is linearly related to the amount of heat to which the plant has been exposed since emergence. A convenient measure of accumulated heat, the degree day, can be computed from maximum and minimum daily air temperature. The degree day requires a base temperature which represents the temperature at which plant development stops. For most wheat varieties the base temperature is 0°C. The true temperature driving plant development is the temperature at the growing point. For field observations of populations of plants, mean air temperature at 1 or 2 m is sufficiently close to the mean temperature of the growing point to provide useful predictions.

For growth chamber work it is more important that the actual temperature of the growing point be determined. Depending on radiant energy load in a growth chamber, crown temperature can be as much as 2°C cooler than chamber air temperature. The greater the radiant energy load the greater the difference in chamber air temperature and actual growing point temperature. With the greater detail of plant observation normally taken in a growth chamber and the low number of plants involved, the true temperature of the growing point should be measured for obtaining accurate temperature-development relationships.

The slope of the linear relationship between Haun stage (leaf development) and accumulated degree days from planting provides the length of the phyllochron interval — the number of degree days required to produce one leaf. Observed phyllochron intervals for wheat range from 50 for a spring wheat to 125 base 0°C degree day per leaf for an early planted winter wheat. During any one growing season the phyllochron interval usually remains constant at the rate established in early vegetative growth. Baker et al.,[8] for example, have proposed a relationship between phyllochron interval and the rate of change of daylength at emergence.

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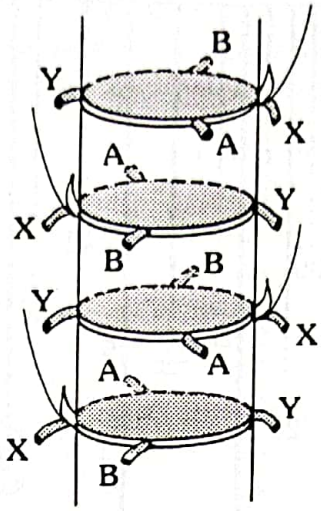

FIGURE 3. Assembly pattern for the wheat plant during vegetative development.

Several different laboratory and field experimental conditions have provided situations in which phyllochrons differed for particular tillers or changed for the mainstem at particular development stages. Seed size was inversely related to phyllochron interval of the first two mainstem leaves in the growth chamber work of Peterson et al.[9] As plants developed their third and later leaves and became independent of seed reserves for growth, all plants produced leaves with the same phyllochron. Rickman et al.[10] demonstrated at low light intensities that phyllochron length was dependent on light intensity. Low intensity (less than 10 mol m^{-2} d^{-1} photosynthetic photon flux density) produced long phyllochrons (greater than 100 degree days per leaf). At higher intensities (20 mol m^{-2} d^{-1} or more) leaves formed at a uniform rate independent of the incoming light. Shading by crop residues was observed to increase phyllochron length in the field by Wilkins et al.[11] In high CO_2 environments (over 600 µl CO_2 l^{-1} air) phyllochrons as short as 40 degree days per leaf occur on some varieties of wheat.[12] Leaves of the mainstem and leaves of tillers normally develop at the same rate, although tiller T0 developed leaves slower than the mainstem in Kirby et al.[13] Water stress is expected to slow leaf development, but extent of slowing and differential effects on tillers have not yet been documented. A computer program named "Plantemp" was produced by Rickman et al.[14] to compute leaf and tiller development for unstressed conditions. Leaf length sizes, available by default in the program or hand entered, permit estimating shaded soil surface area for a seedling small grain crop as a function of growing degree days (GDD) (air temperature) after planting.

VII. DEVELOPMENT ABNORMALITIES

Many field, greenhouse, and growth chamber conditions occur where wheat plants do not form all possible tillers. Imperfect seedbeds, deep planting, nutrient deficiency, small seeds, diseased seed or seedlings, low sunlight intensity, and other problems will reduce tiller formation. The absence of tillers, if analyzed with respect to the expected tillering pattern of Figure 4, provides a quantitative measure of "stress" as caused by the various growth environments.

During the normal tillering process each tiller as identified in Figure 4 will occur within ±0.5 leaves or less of the mainstem growth stage listed in Table 1. If a tiller does not appear during this interval it will usually not appear at all. Growth stress occurring during the expected

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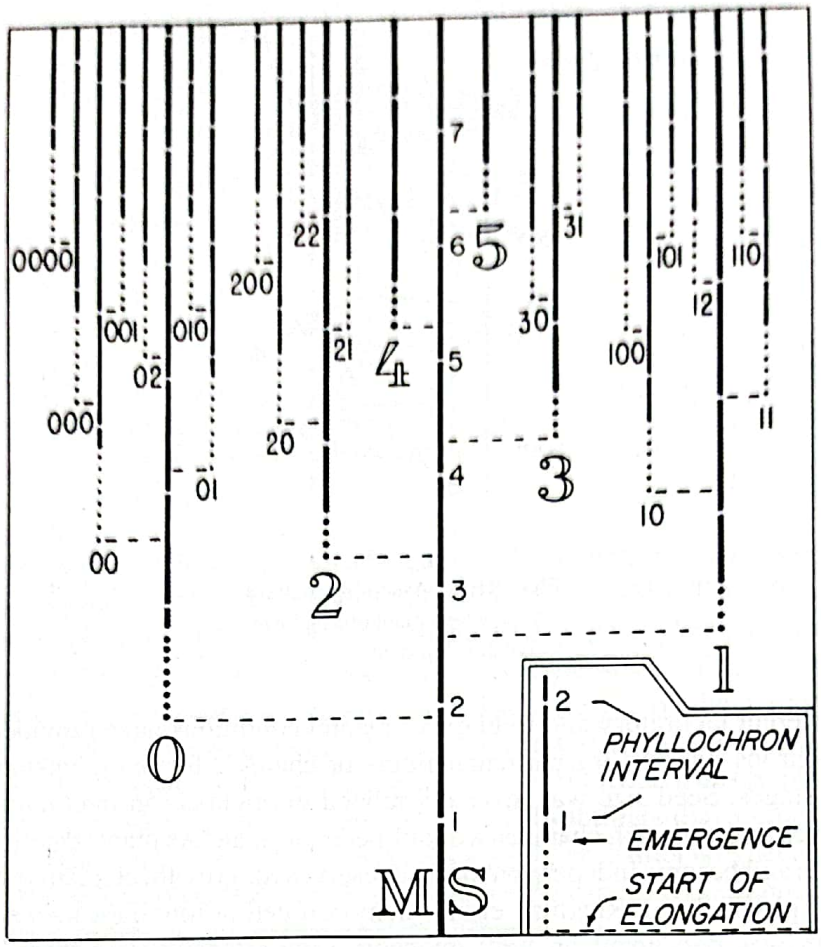

FIGURE 4. Relationships of leaf and tiller appearance in winter wheat. The passage of phenological time is measured in elapsed phyllochrons which are numerically equivalent to the mainstem Haun stage.[1]

appearance interval of any tiller will cause that tiller to be skipped. If the environment turns favorable at a later time, it will be the tillers scheduled for appearance during that later time — as determined by the mainstem growth stage — that will develop.

In a field, not all plants are at the same developmental stage nor do they experience identical environments. Therefore, in a generally stressful situation there will be a fraction of all plants that experience stress sufficient to cause a tiller to be skipped. The higher the fraction of plants in a field that skip a particular tiller the more severe or the more uniform was the stress situation.

The precision with which tillers normally do appear with respect to their characteristic mainstem Haun stage makes it possible to use after the fact observations of wheat plants to determine the timing as well as the intensity of stresses experienced by the plants. For example, plants sampled at Haun stage 7.5 have had the opportunity to develop all tillers through T5. If only 50% of the plants formed T1 and 90% formed T2, one can conclude that a stress sufficient to suppress tiller formation to 50% during the formation of T1 was relieved to the extent that only 10% of T2s were suppressed. The stress occurred about $4^1/_2$ phyllochrons before the sampling date. (Tiller T1 is expected at about Haun stage 3.0.) With a phyllochron of 100 degree days, which is a good rule of thumb value for fall-planted winter wheat, daily air temperature records for computing daily and cumulative degree days would allow retracing calendar dates back to the time when the stress occurred. Weather, field conditions, or cultural events associated with that time are logically suspect as the source of the stress.

Tiller T0 is the most sensitive to environmental stresses. Peterson et al.[15] determined the effect of seed size, seed damage, and seedling-light capture on fractional appearance of T0. Small

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TABLE 1
Mainstem Haun Stage at which Tillers are Expected to Appear

Tiller ID	Mainstem Haun at tiller appearance
T0	2.8
T1	3.1
T2	3.6
T00	4.2
T3	4.7
T01	4.8
T10	4.6
T4	5.7
T02	5.8
T11	5.4
T20	5.1
T5	6.7
T12	6.4
T21	6.0
T30	6.1
T001	6.3
T100	5.9

seeds, damaged seeds, low light intensity, or leaf L1 removal as it appeared eliminated T0 formation. Tiller T0 and, to a lesser extent, T1 are skipped in deeply planted seedbeds. Any environmental condition that limits the carbon resources available to the tiller at its scheduled time of formation seems to limit the fraction of plants that develop that tiller.

VIII. RELEASE OF APICAL DOMINANCE

Several naturally occurring or artificially imposed conditions will interfere with the normal tillering order and the normal size relationship among the parent culm and tillers. Tiller size normally follows an expected hierarchy of oldest; first developing tillers are biggest. Any insect, disease, or physically caused death of the parent tiller tends to release any pattern of dominance and any of the older tillers may become the dominant culm for the plant. Accurate identification of tillers on damaged plants, particularly those damaged by growth-substance-creating insects like the Hessian fly, can be extremely difficult.

Purposeful interference with normal patterns is sometimes used to study the mechanisms controlling tillering. Artificially applied auxins or auxin antagonists, cytokinins, or gibberellic acid have been used[3] to modify tillering patterns in search of causative mechanisms. Apparently, a combination of internal growth substances as well as carbon and nutrient availability interact to provide the controlled tillering pattern.

IX. NORMAL TILLER ABORTION

A wheat plant with adequate or currently excessive nutrition will develop more tillers than it can support to maturity. The overproduction of tillers seems to be a survival mechanism allowing the plant to take advantage of early plush growing conditions and permitting a natural thinning of culms if environmental stresses appear.

Often the majority of tiller abortion takes place before water supplies become limiting to growth in the Pacific Northwest. When the wheat plant begins its reproductive stage (when head formation begins at the growing point of the main culm), those tillers with fewer than three fully expanded leaves will be aborted. The timing of the loss of these small tillers may vary from the beginning of double ridge to jointing — the beginning of stem elongation.

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Only close examination of the tillers between double ridge and jointing will detect their imminent demise. The most reliable observation of tiller abortion is a plot of tiller Haun stage vs. cumulative degree days. Tillers that are being aborted will exhibit a gradual decline in, and ultimately a zero value for, their leaf development rate. Even though elongation has ceased, the leaves of these aborted tillers will remain green for a week or two, but will gradually senesce and dry as the surviving culms mature.

X. STRESS INDUCED ABORTION

Tiller appearance is no guarantee that the tiller will survive to produce a head or even to jointing. If resources are limited, a plant will respond first by skipping tillers. As limitations become more severe, the plant responds by aborting tillers that are already present, starting with the youngest or latest developed tiller on the plant. Nutritional shortages, water shortages, crowding, or shading by competing plants have been observed to cause the death of small tillers.

Occasionally, under severe nitrogen or water stress during boot and heading, some of the tillers that survived jointing will also be aborted. Normally, if a tiller survives jointing, it will produce a head with some grain.

XI. PHENOLOGICAL STAGES

The early vegetative development of wheat is precisely described and timed by the combination of mainstem Haun stage, known tiller developmental pattern relative to mainstem Haun stage, and linear relation between cumulative degree days from planting or emergence, and mainstem Haun stage. During the first 200 to 300 degree days after emergence, the plant is an untillered seedling. Depending on seedbed quality, tillering will begin with T0 as the leaf L3 is forming, with T1 as leaf L4 begins, or with T2 as L4 is completed. Increasingly larger groups of tillers and subtillers appear during successive phyllochron intervals. The better the seedbed conditions and the shallower the seeding, the greater is the probability of forming T0 and T1; therefore, the earlier the tillering stage begins.

The single ridge, double ridge, and apical spikelet or jointing[16] of the reproductive stage occur in the spring of the year under conditions dependent upon the degree of spring growth habit and daylength sensitivity of the variety. For a fully vernalized winter wheat with moderate daylength sensitivity, single ridge will usually occur in the interval between 1 and 2 phyllochrons after daylength begins to increase in winter. January 1 is commonly used as the beginning of increasing daylength for the northern hemisphere. Double ridge in winter wheat will occur about 1 phyllochron after single ridge, and jointing in winter wheat will occur about 2 phyllochrons later. Using the rule of thumb that phyllochron length is 100 degree days, single ridge is expected to occur from 100 to 150 degree days after January 1. Double ridges should form between 200 to 250 degree days and jointing should occur from 400 to 450 degree days after January 1.

Developmental stages later than jointing are dependent upon the flag leaf number of a plant. Flag leaf number is determined for winter wheat at the time of single ridge. An early fall planting will produce many mainstem leaves, and therefore the flag leaf number can be large (13 or above). Late fall or early spring planting will result in only a few mainstem leaves with a correspondingly small number for the flag leaf (8 to 10). It will be a number that is about twice the mainstem Haun value at single ridge. As a first approximation, the number of phyllochrons from emergence to single ridge will equal the number of phyllochrons from single ridge to flag leaf extension or the very first of boot stage. Boot stage will be followed by heading and each will be about one phyllochron in length. Anthesis is expected from the completion of heading to about one half of 1 phyllochron after heading stage is complete. The kernel-development stage intervals are strongly dependent upon specific variety, location, and weather interactions, but are frequently approximated by constant degree day intervals for each. Occasionally, degree

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days computed with a base temperature specific to the grain filling interval are used. Much early work that simply correlated degree days and various growth intervals is summarized by Nuttonson.[17]

For spring wheat where the number of the flag leaf is commonly 7 or 8, the same principles used to project winter wheat reproductive stages can be used. On a variety with the eighth leaf as flag leaf, single ridge would be expected no later than between Haun stages 3.0 and 4.0. Double ridge would be 1 phyllochron later and jointing only 1 phyllochron after double ridge. Double ridge to jointing in spring wheat is shortened to about half that in winter wheat and spring wheat heads form fewer spikelets in that interval. Later stages are projected as for winter wheat.

XII. ALGORITHMS

A. DEGREE DAYS

Definition (variable name) [units]

Degree days (DD) [base 0°C degree days]
Maximum temperature (T_{max}) [C]
Minimum temperature (T_{min}) [C]
Base temperature (T_{base}) [C]

Algorithm:

$DD = ((T_{max} + T_{min})/2) - T_{base}$

Comments:

For following or projecting wheat development in the field, daily air temperature from an adjacent or representative weather station, using the Celsius scale with zero base temperature, is adequate. For growth chamber or greenhouse work where detailed development is observed, true crown or growing point temperature is more important.

B. CUMULATIVE DEGREE DAYS

Definition (variable name) [units]

Cumulative degree days (CDD) [base 0°C degree days]
Day of the year (day) [day of the year from January 1]
Degree days occurring on each day of the year
(DD[day]) [base 0°C degree days]
First day of an accumulation interval
(dayfirst) [day of the year from January 1]
Last day of an accumulation interval
(daylast) [day of the year from January 1]

Algorithm:

CDD = SUM from dayfirst to daylast (DD[day])

Comments:

SUM represents the mathematical summation.
Dayfirst for most Haun calculations is the day of planting.

C. MAINSTEM HAUN DEVELOPMENT STAGE

Definition (variable name) [units]

Haun stage of mainstem (Hms) [leaves]
Phyllochron interval (Phyllo) [base 0°C degree days]

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Emergence requirement (Emerg) [base 0°C degree days]

Algorithm:
Hms = (CDD - Emerg)/Phyllo

Comments:
This assumes that Phyllo is constant throughout a growing season.

D. MAXIMUM TILLERS ON A PLANT

Definition (variable name) [units]
Maximum possible tillers per plant — mainstem included (Tlrmax) [a count]

Algorithm:
Tlrmax = 0.4472 * (1.6180)^Hms

Comments:
This is known as Binet's formula for approximating the Fibonacci series.[12]

E. TOTAL NUMBER OF LEAVES ON A PLANT

Definition (variable name) [units]
Number of leaves on a plant (Lfno) [a count]
First tiller to form on plant (firstiller) [a count]
Last tiller to form on plant (lastiller) [a count]
Tiller identification (tlr) [a name]
Haun stage of a tiller (H[T/r]) [leaves]

Algorithm:
Lfno = Hms + SUM from firstiller to lastiller (H[tlr])

Comments:
If tillers are missing they must be omitted from the summation.

F. NUMBER OF PHYLLOCHRON INTERVALS FROM JANUARY 1 TO VARIOUS DEVELOPMENT STAGES

Definition (variable name) [units]
Mainstem Haun stage on January 1 (Hms[Jan. 1]) [leaves]

Algorithm:
Single ridge is about
(1-[Hms(Jan.1)-INT(Hms(Jan.1))]+1) after January 1 [phyllochron]
Double ridge is about 1 phyllochron after single ridge
Jointing is about 4.0 to 4.5 phyllochrons after January 1
Boot stage is the first Haun stage to follow extension of the flag leaf

Comments:
In Haun's original scale two intervals are defined between flag leaf and heading: (1) flag sheath or extension and (2) boot.
Heading stage is the Haun stage immediately following Boot.
Anthesis occurs approximately one half phyllochron after heading is complete.
INT ( ) is the integer function.
January 1 is used for the northern hemisphere.

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Chapter 8

PREDICTING ROOT DEVELOPMENT OF CROP PLANTS

Betty Klepper and R. W. Rickman

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I. INTRODUCTION

This chapter discusses general patterns of development of crop root systems and modeling concepts used to predict rooting over a cropping season. Rooting parameters of interest to most modelers are rooting depth and/or the root length density profile as related to time. Other parameters such as root surface area or dry weight distribution with depth can usually be calculated from the root length density profile if the distribution of root diameters is known. This chapter, however, concentrates on rooting depth and root length density profile.

II. ROOT DEVELOPMENT PATTERNS OF CROP PLANTS

A. INTRODUCTION

Since most crop plants are annuals, root system development patterns begin with elongation of the radicle from the seed. In monocots, this initial axis is followed by a series of axes produced from successively higher nodes on the stem. Thus, the root system is made up of many axes and their branches.[1] Earlier axes are usually the most deeply rooted and most highly branched because they have had the greatest length of time in which to explore the soil profile and develop morphologically.[2] In dicots, the radicle may give rise to a taproot with associated laterals and their branches, or it may produce a diffuse root system when several strong lateral roots take over the lead of the taproot.

Figure 1 diagrams the root patterns of each of these three types of root system. This figure divides roots into three classes. The first class, A, is the downward-growing taproots, axes, or main laterals which serve primarily for transporting roots during most of the life span of the root system. Although they do absorb materials early in their life, these roots serve to transport water and minerals absorbed by branch roots to the shoot and to deliver carbohydrates to the young roots and growing tips over most of their life span.

The second, or "B", class generally consists of first-order lateral roots. These may be horizontal or vertical and may grow obliquely for a while and then turn vertically downward. The function of "B" roots includes both transport and absorption, depending on the species and the time in the season.

The third class is "C" roots which are primarily absorbing roots. These may be ephemeral. Generally they consist of laterals of secondary order.

B. MONOCOTS

Monocot root systems consist of main axes which primarily grow downward and lateral branches of these axes which may grow in any direction, but are produced at right angles to the parent root and usually grow for at least a time in this orientation. Main axes are produced from nodes on the plant stem. As each node passes through its developmental sequence, it produces axes at set points in developmental time. This provides a continuous series of potential axes over time. Surface soil conditions are important in determining the success of each potential axis.

In the grass family, these nodal roots consist of seminal roots, which arise from primordia present in the embryo, and crown roots, which arise from the lower vegetative nodes.[1] Generally, for the grass family, crown roots elongate by the three-leaf stage.[3]

For wheat, the seminal root axes consist of the primary root and up to five roots associated with the two nodes in the seed. Roots from the coleoptilar node may also originate at planting depth and become confused with seminal roots.[4] Foliar nodes give rise to crown roots which are produced from successively higher nodes as the seedling develops.[1,5] Generally there are two to four axes per node.[6]

Figure 2 illustrates a naming system for cereals. This system references each axis to its node of origin and indicates a direction of growth with respect to the other plant organs associated with the node. In wheat, each of the lower nodes produces a pair of roots (for the nth node, nA and

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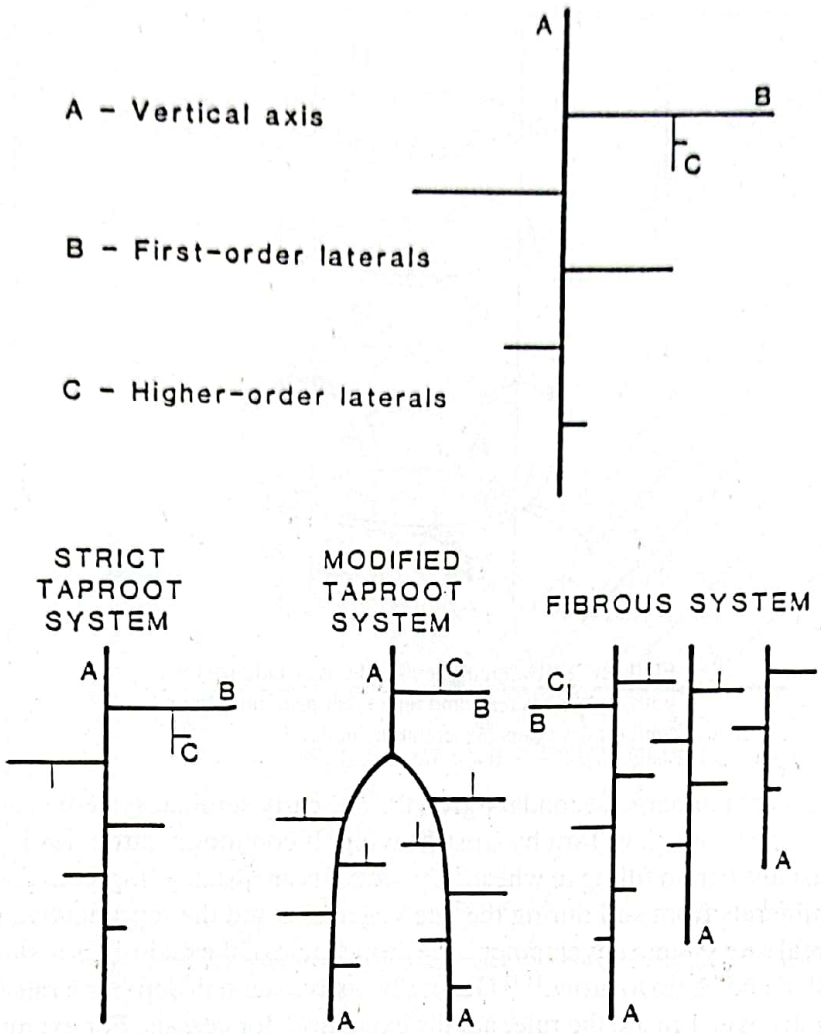

FIGURE 1. Classes of roots which comprise a root system.

nB) on either side of the stem at right angles to the bud associated with that node. Later in development, the plant can produce another pair of roots (nX and nY) at right angles to the first pair (Figure 2).

The unique relationship between monocot stem nodes and crown root axes permits correlations between shoot and root development to be derived. For example, Figure 3 shows the degree of branching found on individually identified wheat root axes and the number of leaves on the mainstem as a function of phyllochrons after emergence.[1] A phyllochron is the unit of time between equivalent growth stages of successive leaves, e.g., between a visible leaf number of n and n+1. This diagram shows that each segment of root length produces branches about 2.5 phyllochrons after it first appears. Since each phyllochron requires approximately 100 growing degree days (GDD),[7] the appearance and branching of wheat root axes can also be predicted from cumulative GDD. Cumulative GDD is calculated by summing the average air temperatures in degrees Celsius for each day with all negative means taking a value of zero. A plant sampled 600 GDD (6 phyllochrons) after emergence would be expected to have 6 mainstem leaves, well-branched seminal root axes, and a crown root system with branching only on the axes associated with the first foliar node (Figure 3). Rice[8] and corn[9] have similar root systems comprised of axes associated with nodes.

The development of a monocot root system, then, can be described in terms of the production of a sequence of root axes and their subsequent branching. Axes from higher nodes tend to grow out to the side before going downward so that they explore ever-widening rings or cylinders of

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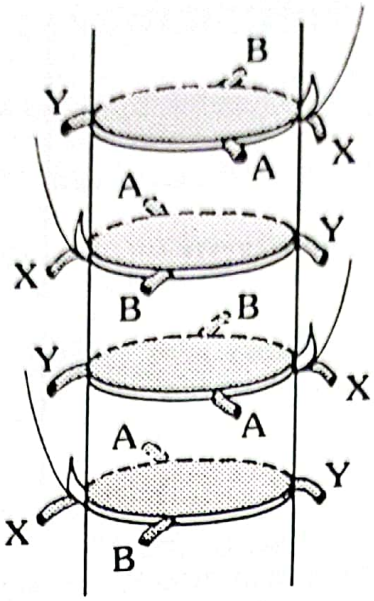

FIGURE 2. Diagram showing the association of roots with nodes in cereals and relationships of nodal roots with other organs present at the node.

soil. Monocots do not undergo secondary growth. The early seminal system is not persistent if subjected to pathogen attack or torn by frost-heaving. It commonly atrophies in corn.[10] It can, however, persist until grain filling in wheat.[7] Crown roots are usually important in the extraction of water and minerals from soil during the late vegetative and the reproductive periods.

Early in cereal root system development, the growth rate of the main axes is slowed as branch roots are initiated and begin to grow.[11,12] Generally, axes extend in depth at a rate of about 1 cm/d. Rooting depths over 1 m are the rule, not the exception, for cereals. For example, Weaver et al.[13] report winter wheat root depths of 5 to 7 f (1.5 to 2.1 m) in Nebraska. The length of root material produced by a cereal crop is also high. Values of over 15 km/m^2 of land surface for corn[14] and over 10 km/m^2 for wheat[15] have been reported.

C. DICOTS

Root systems of dicotyledonous annuals are either taprooted or have been modified to form a diffuse root system. Taproots explore ever-deeper layers of soil over time, may undergo secondary growth, and may be decidedly woody. Most dicot roots are capable of secondary growth and develop complex vascular relationships among parent roots and their branches. In soybean, laterals from the taproot grow horizontally or obliquely downward for a time and then turn vertically downward.[16] They may be absorptive early in their life span but later become transporting roots.

Dicots may be deep-rooted. Kaspar et al.[17] found that all seven soybean cultivars studied in a rhizotron experiment reached the compartment bottom at 2.2 m. As a general rule, dicots produce less root length in a growing season than cereals do. For example, Barber[18] found that soybean root density was about 20% of the root density of corn grown in the same field. He found the maximum soybean root length to be 2.4 km/m^2 of land surface on a Chalmers silty clay loam soil. This value was nearly the same as the 2.5 km/m^2 found by Sivakumar et al.[19] on an Ida silt loam. Note that these values are much less than the 10 to 15 km/m^2 for monocots.

D. ROOT BRANCHING

Branch root initials arise in the outermost cell layer (pericycle) of the stele about 10 to 20 mm proximal to the root tip. These initials then begin to grow and literally tear their way out of the

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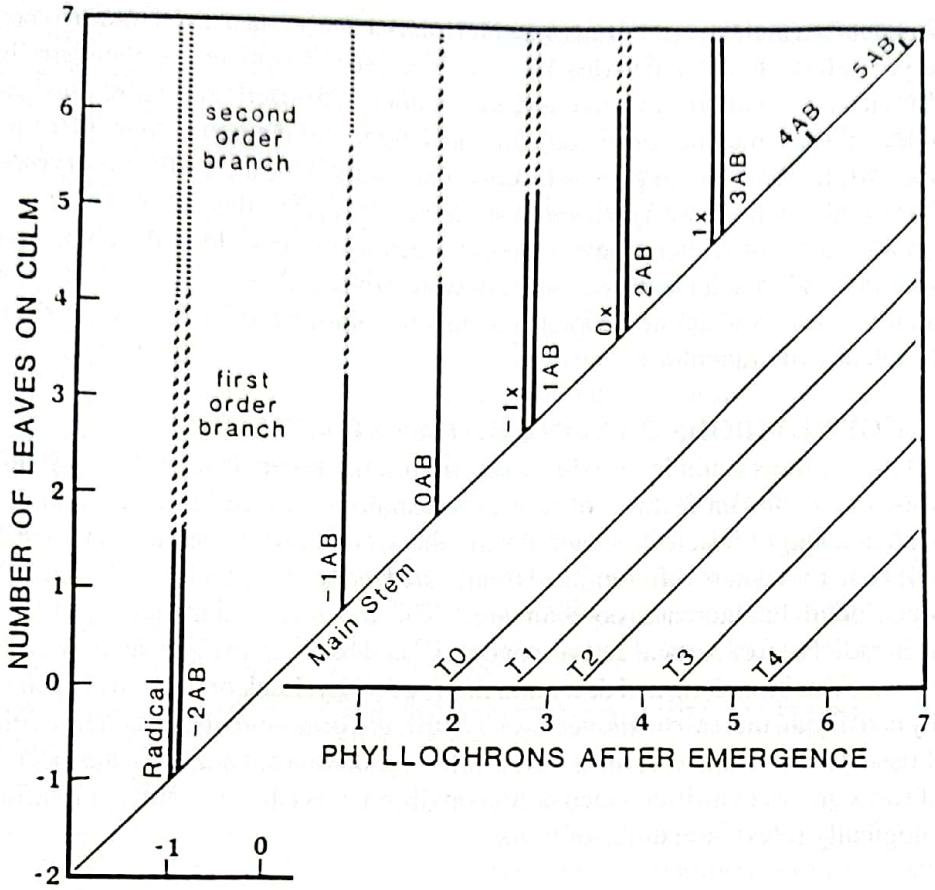

FIGURE 3. Root axis production and branching as related to shoot development and GDD from emergence.

parent root as a result of growth pressures generated. As the distal end of the new branch root presses outward through endodermal, cortical, and epidermal layers, the proximal end differentiates to produce xylem cells which abut the already matured xylem of the parent root. This junction of new to old xylem is a potential site for resistances to water flow in the soil-root-shoot pathway.[20] Water and minerals taken up by the lateral root must pass across this junction in monocot roots which have no secondary growth. Many dicot roots have secondary growth so that smooth elbows of xylem tissue are laid down to carry the xylem sap smoothly from the lateral root up the parent root in a continuous linear series of xylem elements.[20] Presumably, this structure offers less resistance to flow than does the monocot junction.

Timing of branch appearance is controlled primarily by tissue maturation; i.e., root branch initials will not differentiate prior to a set point in tissue maturation. Both field and laboratory observations suggest that there is a window of time during which lateral roots grow out from a particular segment of root. Generally, when root systems are extracted from soil or from potting medium, the proximal lateral roots are progressively older, longer, and more branched than are the distal ones. Rarely do we see a mixture of old, branched laterals and young, fresh laterals. Therefore, there appears to be a limited time window for a root segment to produce lateral roots. For controlled-environment growing conditions, this means that lateral roots will appear at a specific time after the root hairs grow out and that the distance between the root tip and the point of appearance of the newest lateral is generally constant for the conditions selected. For field conditions, a combination of time and temperature must be used to time the period between initial growth of a segment of root and the appearance of lateral roots.

The linear frequency or density of lateral roots (number per centimeter) also varies with species and culture conditions. There is an effect of nutrients,[21] with especially marked decreases

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under severe nutrient deficiencies.[22] Legumes and maize have about 5 and 8 roots per centimeter, respectively,[23] radish 5 to 6,[24] and barley 1.7 to 3.7[25] or 5 to 6.[26] Apparently, there are significant effects of environment on linear frequency, even under optimized laboratory conditions. The number of lateral roots may be correlated with the diameter of the parent axis.[27] Unfortunately, most data are from laboratory experiments concerned only with the earliest roots of seedlings with experimental conditions very different from those found in the field.

Intact root systems of winter wheat were extracted from the field at different times in the growing season.[28] Individual identified root axes were examined for degree and linear frequency of branching. Those axes which developed branches after spring fertilization showed an increase in linear frequency of branching.[2]

E. EFFECT OF ENVIRONMENT ON ROOT ANATOMY

The anatomy of roots is not immutable. Soil environments can have profound influences on the physiologically relevant features of roots. For example, changes in temperature can affect root diameter and length,[29] stele diameter and number of metaxylem vessels in maize,[30] and the region of the bean root where differentiated tissues are first seen.[31] Mechanical impedance tends to reduce root length but increase root diameter.[32] This increase in diameter is primarily due to an increase in radial size of cortical cells in soybeans[33] and barley.[34] In dry bean roots, mechanical impedance increases branching and decreases tissue porosity. Lack of oxygen also changes root anatomy by causing an increase in tissue porosity through formation of large intercellular spaces in cortical tissues. Unfortunately, most of our information on root anatomy has been based on sections of roots grown in artificial media. Soil environments can have profound influences on the physiologically relevant features of roots.

F. ROOT SENESCENCE

Although many roots of crop plants persist throughout the season, some branch roots senesce and decay. This root "turnover" is a normal part of root system development. We do not know what the physiological and anatomical distinctions are between long-lived and ephemeral branches. In dicots, some branches undergo secondary growth and become a part of the framework of the root system; others do not undergo secondary growth and senesce. In cereal axes, the cortex is normally short-lived,[35] but the stele and endodermis persist. Fusseder[36] found that corn laterals with dead tips could remain functional and that the cortex of the main seminal root was still alive at the late grain filling stage.

III. ROOT-SHOOT RELATIONSHIPS

Roots cannot be modeled without reference to the shoot, which is interdependent on the root.[37] Only if the shoot is growing and functioning "normally" will the roots receive the necessary materials for the growth of new root length to provide the new sources of soil materials for shoot growth. Generally, root to shoot ratios are high for seedlings, decrease during the growing season and are low at maturity. For example, Anderson-Taylor and Marshall[38] found that the root to shoot dry weight ratio of spring barley (*Hordeum distichum* L. Lam.) was about 0.3 1 week after planting and decreased to 0.1 over the next 11 weeks.

For grasses, partitioning of dry matter between roots and shoots changes during the reproductive phase. Stem elongation and grain filling reduce the dry matter partitioned to roots. For example, Parsons and Robson[39] found that partitioning of assimilate to roots decreased from about 12% to less than 4% during spring growth of perennial ryegrass (*Lolium perenne* L.).

There are feedback mechanisms for maintaining shoots and roots in relation to one another. This interrelationship can influence crop rooting patterns in field soils. For example, water stress generally reduces shoot expansion at a milder level of stress than it influences photosynthesis. Under mild water stress, roots still receive photosynthate from shoots and elongate new root

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material wherever soil conditions are favorable, even when shoot expansion is depressed. Similar rules apply to nutrient deficiencies in general: they affect shoots more than and sooner than they do roots. Severe stresses affect root growth by effects of shoot stresses on carbohydrate supply. Factors such as shading of plants by weeds can decrease carbohydrates available for root proliferation. Also, in some species there is a decrease in root growth rate when growth of reproductive structures causes a diversion of assimilate away from the below-ground plant. For example, total root length of corn increased until silking (80 d), remained constant for 14 d, and then declined.[14] Similar observations have been made for other species where measurements have shown either a cessation of growth or a slowing of root growth rate after pollination.

Roots can either be directly attacked by plant pathogens or indirectly affected by the influence of shoot pathogens on shoot physiology. For example, powdery mildew (*Erysiphe graminis* f. sp. hordei Marchal) causes reductions in photosynthetic leaf area directly, but indirectly affects root dry weight and length primarily through effects on laterals.[40]

Direct effects of soil-borne pathogens on roots are primarily from suppression of root elongation rate (e.g., inhibitory *Pseudomonads* as described by Frederickson and Elliott[41]), actual consumption of root material (as, for example, cutworms or other larvae), distortion of root tissues to make them less effective (such as rootknotting types of nematodes), and, the most common case, from rotting of roots by such organisms as *Pythium* or *Rhizoctonia*.

IV. ROOT-SOIL GROWTH RELATIONSHIPS

A. INTRODUCTION

Soil conditions are the most important factors to quantify in order to predict either rooting depth or root length density profiles. Unfortunately, the soil conditions most important to root elongation are dynamic, very difficult to measure, and interdependent. For example, soil strength must be relatively low for root cell elongation to occur, but soil strength depends not only on soil bulk density, a relatively static factor, but also on soil water content, a highly dynamic factor. Also involved are the soil gaseous diffusion rate for oxygen, soil temperature, and soil water potential. Certain soil chemical conditions such as high osmotic potential, high activities of certain ions such as aluminum, and pH can also affect root elongation rate. For most agronomic situations, soil physical factors predominate as limiting factors.

B. ROOT ELONGATION PHYSIOLOGY

Root elongation takes place due to the longitudinal enlargement of cells immediately behind the root tip. The driving force behind this elongation is the turgor pressure in cells of the elongation zone. Resisting the force applied by turgor are cell wall constraints and constraints (strength, friction) of surrounding soil. An expression of these relationships is

$$\frac{1}{L}\frac{dL}{dt} = \emptyset(P-Y-M)$$

where:

L is root length
t is time
Ø is wall extensibility
P is turgor pressure
Y is the threshold turgor needed for cell expansion
M is the soil resistance to root penetration

Although all of the terms in this equation may change over time, the term which changes the most

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is soil resistance to root penetration (M). This factor depends at a minimum on soil water content, bulk density, and soil texture. Thus, root elongation models must contain at least some empirical factors. For example, Jones and Bland[42] account for changes in soil resistance using soil texture, water content, bulk density, aeration, and temperature.

For a typical root in moist, loose, friable soil, the length of the elongation zone (L) is of the order of 5 mm and elongation rates (dL/dt) are about 1 mm/h. A value for Ø of 0.24 MPa h^{-1} has been obtained for pea internodes.[43] Using this value for roots, the net pressure for elongation would be about 0.8 MPa. This net pressure might arise, for example, from a cell osmotic pressure of 1.2 MPa and a water potential of -0.1 MPa to give a net cellular turgor pressure (P) of 1.1 MPa with a 0.2 MPa yield threshold (Y) and a 0.1 MPa root-soil frictional resistance term (M). Unfortunately, these values are extremely difficult to measure, especially in field soils, and they all may vary with changes in soil environment or with endogenous plant factors. For a particular soil type and plant species, an empirical approach[44] can be used to estimate root elongation rates. In this approach, the relative rate of root elongation is calculated from the penetration resistance of the soil, which in turn is calculated from empirical relationships of penetration resistance to soil bulk density and water content for the particular soil type.

C. REQUIREMENTS FOR ELONGATION

In order to maintain high rates of cell elongation, roots need adequate energy, which requires oxygen for oxidative phosphorylation. If soil air oxygen concentration is below about 3% or if compaction and/or waterlogging causes the soil oxygen diffusion rate to fall below a critical threshold, root elongation will slow and eventually cease. The presence of a water film around the root itself is very restrictive to oxygen supply rate because the rate of oxygen diffusion through water is 10^4 slower than through air. Some oxygen can be supplied from the shoot in those roots which develop perenchyma. Production of these air-filled spaces is increased in many species in response to water logging.

Biosynthesis of new cell materials such as membranes and wall materials is one of the growth processes which requires large amounts of oxygen. Large amounts of carbohydrates are also required as a base material for these syntheses. This photosynthate is delivered to the growing root tip via the phloem, which is mature relatively close to the root apex. Carbohydrates released from phloem must move across the tissues of the root, presumably by diffusion. Little is known about partitioning processes which allocate materials to the different growth points of the root system; nor do we have good measurements of the storage of carbohydrates within growing root systems. Nevertheless, it is logical to assume that root elongation rate can be limited by the rate of supply of photosynthate.

Another energy-requiring process is the active and selective accumulation of ions from the surrounding soil solution. Under laboratory conditions, at least, there is a decrease in root surface pH which coincides with the elongation zone and is probably associated with proton efflux from the growing tissues.[45] Ions taken into root cells serve, along with sucrose and other sugars, to maintain osmotic potential in cells of the elongating zone. This osmotic potential is necessary to maintain the "P" term in Equation 2. Osmotic potentials of elongation zones generally range from about -8 to -12 bars.[46]

One ion crucial to root growth is calcium which is required in the elongation process.[47] Without sufficient calcium, roots are thickened, distorted, and have poor development of laterals.[48]

Rapid root elongation in soils can only be sustained if there is a rapid radial influx of water from the surrounding soil solution. This water movement takes place down a water potential gradient. The control of this process is still being elucidated, but wall-yielding is thought to be of central concern in controlling the rate of elongation.[49,50]

Root temperature has an important effect on root growth. Temperature affects rates of metabolic processes, diffusion of materials within the growing tip, ion uptake from surrounding media, cell division, and cell enlargement. Hydraulic conductivity of plant membranes de-

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creases with decreasing temperature, making it increasingly difficult to move water into elongating cells as root temperature declines.

Large soil pores provide channels of easy root penetration and may have profound effects upon the shape of a root system.[51] Roots tend to grow along ped surfaces in soils, even when the ped has a relatively low resistance to penetration.[52] Roots grow along the surfaces of cracks, not *in* cracks.[53] Vertically oriented cracks, which correspond to the geotropic orientation of the root, allow the most rapid penetration. The proportion of roots which enter a vertical crack decreases with decreasing crack width and with the approach to perpendicular of the root path to the direction of the crack.[54,55]

When roots penetrate soil materials, they compress the cylinder of soil immediately around themselves.[56] Thus, the elastic modulus or compressibility of soil is an important factor in root growth. This factor is usually measured as soil resistance or mechanical impedance with a penetrometer, which monitors the force required to press a root-shaped probe through the soil. Penetrometers require more force than comparably shaped roots. The mechanical advantage provided by the cone-shaped root cap, the sloughing of root cap cells, the presence of lubricating mucilages at the tips of roots, the presence of localized weak spots in soil, and the circumnutation and flexibility of growing tips all allow roots to penetrate soils with penetrometer resistances greater than the osmotic potentials of their elongating cells. For example, Whiteley et al.[57] found that a penetrometer had to exert a pressure 5.1 times greater than a root tip in order to penetrate a fine sandy loam soil.

Two factors which strongly influence soil resistance to root penetration in agricultural soils are soil compaction (increase in bulk density) and soil water content.[58,59] Both of these influences can be further confounded by concomitant effects on oxygen diffusion rate.[60]

V. ROOTING DEPTH OF ANNUAL CROPS

Rooting depth is probably the most important plant root system parameter. Not that the depth of the deepest root is, per se, important. It is not. However, because of interrelationships among soil properties and root elongation, when main axes (A-roots in Figure 1) penetrate a layer of soil, then that layer soon becomes permeated by a proliferation of the branches of the penetrating axis.

Since most root systems under wet conditions follow an exponential decline of root length with depth,[61] depth of root penetration could predict the "root sink" for water and other soil constituents. Although "root sink" activity is not always proportional to the root length density profile,[62] it often corresponds to root activity and thus rooting depth is the single most commonly required parameter for crop growth models.

For many agronomic situations, rate of root penetration of the profile can be summarized in the rule of thumb: "a foot a fortnight", which corresponds to a rate of soil penetration of about 2 cm/d. This represents a rate often measured under "good" soil conditions. For example, Taylor et al.[63] found that cotton roots reached the bottom of a rhizotron compartment (188 cm from the surface) 80 d after planting for an average rate of penetration of 2.35 cm/d. For corn and tomato grown under similar conditions, the rates were 7.7 and 8.6 cm/d, respectively.[64] Values under field conditions are often somewhat smaller, on the order of 1 cm/d because of the less than ideal conditions encountered in the field.

VI. ROOT LENGTH DENSITY OF ANNUAL CROPS

Root length density (cm of root per cm^3 of soil) is often used in models. This parameter lumps all roots, regardless of diameter or age, into a single number used to express the "root sink" available for removing materials from the soil. Actual root sink activity may not be proportional to the root length density profile,[62] but models that use root length density assume that it is.

Root length density generally declines exponentially with depth under well-watered condi-

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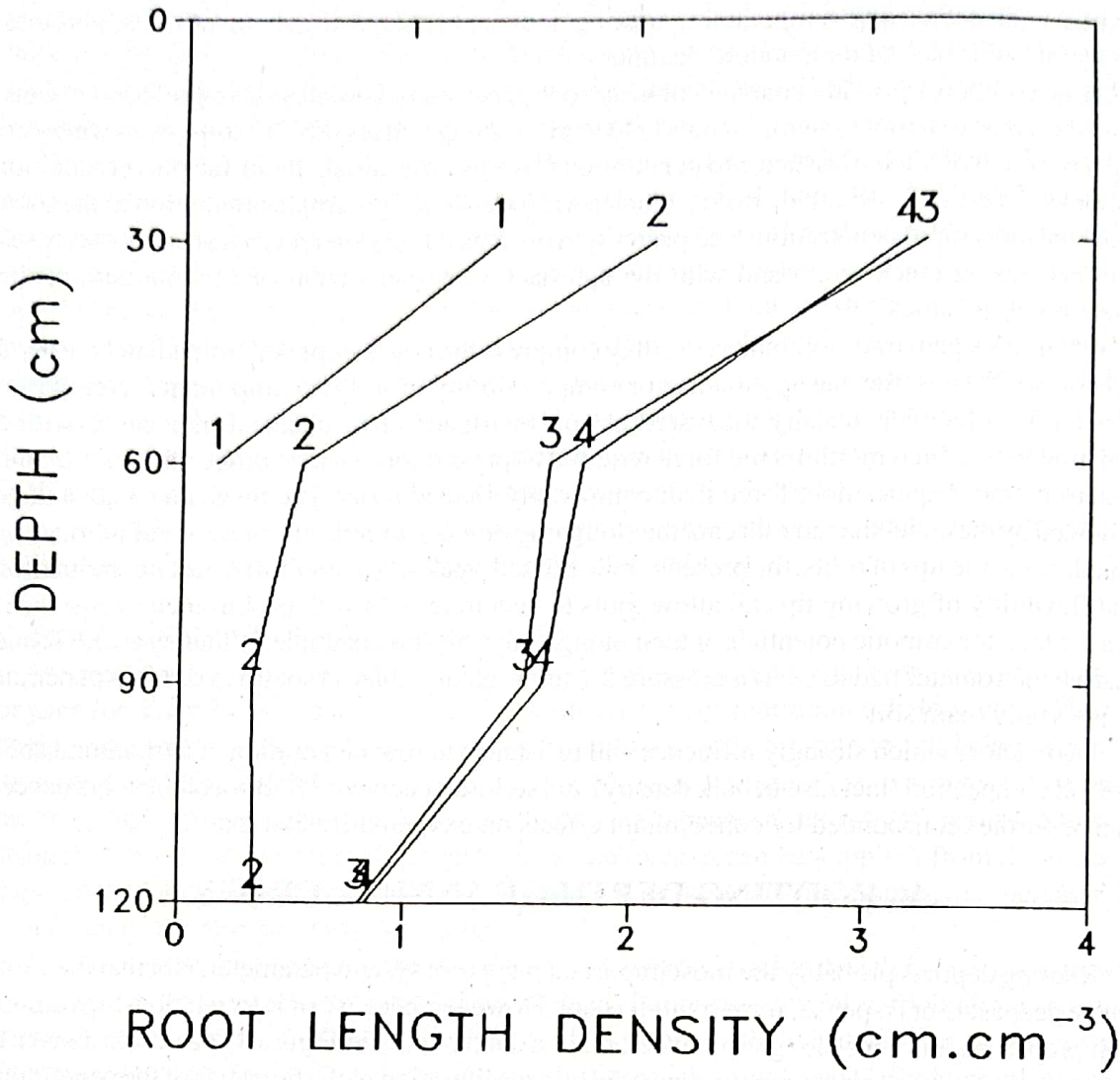

FIGURE 4. Root length density profiles for cotton (*Gossypium hirsutum* L.) taken at 10-d intervals, beginning 75 days after planting in a rhizotron experiment. Data from Browning et al.[79]

tions.[61] This exponential decline would be expected if one assumes that vertical axes produce lateral roots which in turn produce branches. Thus, the upper half of the root length density profile would be made up of axes, their branches, and subbranches and the lower half would always contain a relatively high proportion of fresh unbranched axes.

Figure 4 shows the root length density profile of cotton plants over time under well-watered conditions. Notice that there is an exponential decline with depth at each sampling time. After midseason, the root system remains more or less static. This apparent lack of change is the result of the balance between root decay rates and elongation rates of new root material. Some roots are persistent and others are ephemeral. For example, soybean ephemeral roots have a life span of the order of 2 to 3 weeks.[65] These ephemeral roots pass through growth, maturity, and senescence phases. Therefore, the age composition of roots in a particular layer determines the potential rate of decay of those roots over the next time period. In addition, age composition may control the nutrient absorption capability of the root length present in a layer since young root tips absorb minerals and water at a much higher rate than older sections of the root.

VII. ROOT GROWTH MODELS

In this section some of the current concepts used to generate root growth models for crop

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growth simulations are used to illustrate approaches taken by modelers to date and to illustrate the usefulness of each approach.

A. SOME EXISTING MODELS

One of the earliest root growth models involved partitioning carbohydrates to below-ground biomass. This partitioning coefficient has been assumed by some to be a constant fraction of the daily photosynthate produced and by others to be an amount left over from shoot requirements. One generalized perennial grass model requires roots to grow on the reserve carbohydrate pool.[66] Johnson and Thornley[67] allocated 10% of the carbohydrate to roots in an established grass sward model. A slightly more physiologically based concept is to partition photosynthate to roots as a function of the ratio of root to shoot phytomass. For example, Fishman et al.[68] assumes that sink strength is proportional to sink size as measured by dry matter and partitions photosynthate among the leaves, stems, roots, and tubers of potato according to compartment size. This same general concept is used by Skiles et al.[69] for grasses until senescence, at which time a species-dependent constant fraction of photosynthate is allocated to roots. They also make root respiration rate and mortality dependent on temperature and water stress, lending an environmental sensitivity to the simulation.

Temperature has been used to allocate dry matter to wheat roots with the minimum allocation occurring at the optimum growth temperature and with increasing proportions going to roots as temperatures either rise or fall from 20°C.[70] These authors use a degree day (4°C base) model to simulate rooting depth of wheat. Restrictions from dry soil are obtained by scaling root growth rate from the maximum rate in proportion to how far the soil available water falls below 30% of maximum in the zone into which roots are extending.

Another approach involves both carbon and nitrogen nutrition.[71-73] The partitioning technique used by Reynolds and Thornley[72] adjusts the shoot to root partitioning of photosynthate by the nitrogen to carbon ratio in the labile storage pool of the plant. An additional factor determines the degree of control exerted by the plant on partitioning. Johnson and Thornley[74] incorporated these concepts into a grass crop model which divides root structure into four components (growing, newly expanded, medium-aged, and senescing). This compartmentalization allows calculation of a "live root structural dry weight" and also permits separate uptake parameters and respiratory maintenance costs to be inserted for the different ages of root. The model also makes nitrogen uptake by roots dependent on root content of soluble carbohydrate.

A different approach was taken by Huck and Hillel,[75] who partitioned carbohydrates to roots and shoots according to the relative values of plant water potential in the plant parts. This means that under optimal moist conditions, shoot growth is favored, but roots in moist soil become more favored as the profile dries. Their model also accounts for the effect of local soil temperature. It generates root length by assuming constant relationships between root mass, length, and diameter. Root death depends on soil temperature and the concentration of reserve carbohydrate. These same concepts were incorporated into ROOTSIMU V 4.0[76] which also accounts for decreases in root extension and branching as soil dries.

Of similar complexity is "RHIZOS", a root simulation which generates root length changes daily in small cells (volumes of soil, 1 cm^3) placed specifically with respect to the crop row.[77] Mechanical impedance is calculated for each cubic centimeter of soil and the difference between root turgor pressure and the threshold turgor required for expansion is calculated. These parameters are used to calculate the potential root growth reduction caused by mechanical impedance and soil water potential. Further potential reductions are calculated daily for effects of unfavorable soil temperature and oxygen partial pressures. The most limiting potential reduction is then used to calculate the rate of change of root dry weight in each cell. Finally, carbohydrate left over from shoot requirements is distributed to roots in the soil cells where growth conditions are most favorable.

Jones and Bland[42] have further refined models to express effects of local soil conditions on

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root growth. They address aluminum toxicity and calcium deficiency through user-entered soil-specific parameters, soil texture through a reduction in root growth proportional to the volume fraction of particles larger than 2 mm in diameter, soil strength through input values of soil water content, bulk density, and sand content, aeration through consideration of water-filled pores, critical values of water-filled porosity for the soil, and a plant-dependent factor for sensitivity to flooding, and temperature from the local temperature of each soil layer and a minimum and optimum temperature for growth characteristic of the species. They assume that 1% of the root dry weight in a soil layer dies each day and allow low soil moisture or poor aeration to increase this rate up to a maximum of 2%/d.

A completely different approach is taken in "WHTROOT" by Porter et al.[78] They describe cereal root system growth and development as degree day driven. Each nodal axis develops at a set point in plant developmental time, grows vertically at a constant rate (mm/GDD, $T_B = 0$), and branches after 250 GDD have elapsed. The model contains no restrictions to root growth from stresses. It assumes different rates of elongation, lineal densities, and diameters for different parts of the root system (vertical axes, first-order laterals, and higher order laterals).

B. LIMITATIONS TO MODEL DEVELOPMENT

Development of well-validated root growth and function models awaits improvements in three areas of technology. First, improvements in numerical solutions to complex equations is needed to allow routine use of computers in solving uptake equations. Second, more time-and–cost-effective methods of measuring roots under field conditions will be required before the massive quantities of data required for validation can be obtained. Finally, there is insufficient knowledge about properties of roots and root-soil relationships. Such "simple" questions as, "What fraction of the root system is active in taking up materials?" are not answered. We still know very little about concentrations of materials and other conditions at the root-soil interface. We still do not know the impact of diurnal hysteresis at the root surface on water uptake rates. We have very poor quantitative relationships between root growth and function and numerous environmental factors such as aeration, time of day, and root age. Understanding of the integration of root system activity over the whole profile is fairly good for water uptake where the tensions in the xylem system cause intercommunications among roots, but for uptake of other materials, we know very little about how uptakes are integrated over the entire root system. Morphological and anatomical changes in roots as related to depth in the profile, environmental and endogenous factors, and genetics are only beginning to be studied. Nevertheless, models serve the useful purpose of focusing clear attention on deficiencies in our knowledge and, along with field and laboratory investigations, are an important part of the progress being made toward understanding root growth.

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Chapter 9

MODELING AND PROGRAMMING PHILOSOPHIES

Tom Hodges

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I. BALANCE OF MECHANISM AND EMPIRICISM

Empirical models have a few equations attempting to summarize the crop response to a complex environment with little relation to mechanisms involved in that response. Mechanistic models have a large number of equations that quantitatively simulate or mimic many details of the plant response to the environment. Major factors to consider in choosing between empirical and mechanistic approaches are the error terms in the input data defining the system. If there are large errors in the soil type or soil structure description, soil test data, weather station measurements, weather station distribution (for regional crop simulation), stand density, or pest distribution/density, or if major processes controlling the system are ignored, then accurate mechanistic detail in the processes considered in a model will not make the model more accurate or reliable. Of course, an understanding of the mechanisms can lead to new information about the system that overrides all the background noise involved; it could, for example, lead to a method that completely eradicates a pest or other serious environmental constraint. This is one major reason for studying mechanisms and developing mechanistic models, even when the initial goals of a project might seem to be well served by an empirical model.

A. EMPIRICAL MODELS

The most extreme form of an empirical model is the multiple-regression model, in which variables have been selected solely on the basis of their correlation to the variable to be predicted. Implicit in this type of model are assumptions that measured variables are independent and normally distributed. Although these assumptions are known to be partially untrue, the implications of these assumptions are rarely adequately addressed. Crop modelers should use standard statistical procedures with caution, being aware of all the theory and assumptions involved, and should study and test mechanistic relationships whenever possible, using probability theory to put an error on any model estimate or prediction. Before using a multiple-regression procedure, basic environmental variables (i.e., daily or monthly temperatures, rainfall, solar radiation) should be selected based on our understanding of their physical relationships to the processes to be predicted. The basic variables should then be combined and transformed into new variables believed to be physically related to the problem. Only then should a multiple-regression algorithm be used to select variables from this group of preselected variables based on statistical correlations. A model developed in this manner, in which production of fall and spring planted small grains in Eastern Europe was predicted from monthly temperature and precipitation data is described by French.[1] Some, but unfortunately not all, statisticians emphasize these ideas when discussing use of multiple-regression techniques.

All crop growth simulation models have some degree of empiricism. We neither understand nor are we able to simulate plant growth processes from the highest down to the lowest level (biosphere, ecosystem or cropping system, field or plot, whole plant, plant organ, cell, molecule, atom, or subatomic particle). Whisler et al.[2] suggest that one should not attempt to make a model mechanistic more than two levels below the level at which the model is to predict, i.e., a model intended to predict crop yield for a field should not be mechanistic below the plant organ level. A greater degree of mechanistic detail may make a model more complex than is necessary.

Highly empirical models have the ability to predict growth only over the range of conditions covered by the database used in developing the models. They are prone to large errors when used under different conditions, such as a very different year at the same location or in a different climate region. Models with a smaller empirical component may be used to extrapolate beyond the data used in creating them, provided they are based on sound theoretical assumptions which are correctly implemented in computer code.

B. MECHANISTIC MODELS

Different levels of detail may be appropriate for each part of a model. It appears possible to

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add virtually unlimited amounts of detail to a simulation model to make it increasingly mechanistic. However, the addition of detail is limited by the effort needed to understand growth processes in great detail, by the capacity of computers to run the models, by the amount of time needed to run the models, and by the amount of time needed to interpret the model results. The model developers must continually decide how much detail to add to each model process and when to limit detail. Generally, additional detail should be added only when it will improve the accuracy or reliability of model predictions.

Quade[3] discusses some of the dangers or pitfalls in a quantitative approach to modeling. He mentions "modifying the original real-world problem into another one that fits a particular model or method, rather than tailoring the approach to the original problem; deemphasizing the qualitative aspects or intangible factors in the original problem; using technical, mathematical, and computer language to such an extent that communication fails, except with fellow specialists; and tending to construct such a large central computer model to represent the problem situation that verification becomes difficult or impossible and validation must remain inadequate, while costs in time and money soar." Hodges,[4] in a review of crop yield models, notes that there are always several different approaches to modeling any given problem, which will result in different models.

II. RESEARCH AND APPLICATION MODELS

A. RESEARCH MODELS

Research models are primarily intended to explore the possible relationships among plant growth processes and between the plant and environmental processes. The implications of a hypothesis about these relationships can be investigated by quantitatively implementing the hypothesis in a growth simulation model and examining how related processes would behave if the hypothesis were true. Such simulation studies can suggest experiments and measurements to support or refute the truth of a hypothesis about the interrelationships among various growth processes.

B. APPLICATION MODELS

Application models are primarily intended to predict the occurrence or magnitude of some event. Either a future or hypothetical event might be predicted, such as crop yield at the end of the growing season or after 50 years of soil erosion, or a current or recent event which is difficult to measure directly, such as the degree of soil moisture depletion and how much irrigation water is needed today. There is no clear division between research and application models and probably little value in trying to precisely differentiate between them. We may, however, say without disparaging either type of model that research models are models that are never finished, while versions of application models will be released to potential users at appropriate times during their development cycle and at the end of a project. Successful development of application models is dependent on an understanding of the interrelationships among plant growth processes and environmental processes, largely gained through work with research models.

III. MODULAR PROGRAMMING

A. REUSABLE MODULES, REUSABLE CODE

Modular programming and the new area of Object Oriented Programming Systems or OOPS (discussed in the following section) are closely related. In both modular and object oriented programming, processes being modeled are put in separate sections of a program called modules or objects. These sections carry out single tasks or groups of closely related tasks. Each section has a clearly defined interface with the rest of the program. We can improve or correct modular

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programs relatively easily because the interactions between modules are clear and well defined. No special computer language is needed for modular programming, FORTRAN and other widely known languages are perfectly suitable.

Both modular and object oriented programming are compatible with the concept of building libraries of standard functions and subroutines for crop and soil processes. This concept has been discussed in the crop modeling community since crop modeling began. A group building a model for a particular crop and environment could adapt code from such a library for the bulk of their model, freeing them to concentrate most of their efforts on problems which no one else has solved.

Such a library could contain several functions or subroutines for any process, ranging from somewhat empirical to highly mechanistic. Each function or subroutine should be characterized according to its range of reliability, requirements for input data, and the form of its output data. Programming techniques that tend to result in reusable program modules have been a topic of extensive research in the computer science field.

Creating a model in the form of reusable modules or subroutines with features making it applicable to a wide range of problems is generally more difficult than preparing a model for a specific problem. However, once a library of reusable modules has been established, the extra labor required to make reusable modules should be less than the labor saved by being able to use other people's modules for large portions of a model.

The modeling field is held back when efforts put into developing one model make a minimal contribution to developing other later models. This will happen to the degree that modular programming techniques are not used. Scientists have the opportunity to develop models so that others can easily use components of their models in later work. When a model is designed with processes or related groups of processes isolated in program modules and with well-defined interfaces with other parts of the model, then these modules can be easily adapted for other models. If each process in a model is scattered around in the program, intertwined with many other processes, then much effort will be needed to make further use of the model and it will make a relatively slight contribution to the development of other models no matter how accurate its predictions may be in the range of situations where it can be used.

B. OBJECT ORIENTED PROGRAMMING SYSTEMS

The most recent major trend to appear in programming techniques is OOPS. Many personal computer software companies (Microsoft, Borland International, IBM, etc.) are adding OOPS capabilities to their major language products (C and Pascal compilers so far) or licensing OOPS tools from newer, smaller companies to be sold with their compilers.

With OOPS, a program is constructed from special modules called objects, each of which performs a specific task or group of tasks on a data set. From each object, daughter objects can be derived by adding new characteristics to the parent object. Thus from an object such as "plant organ", daughter objects can be derived that have all of the characteristics of the parent object "plant organ" and have additional characteristics as well. From "plant organ" one could derive "leaf", "stem", and "root". From "leaf" one could derive "growing leaf", "mature leaf", "senescing leaf", and "dead leaf". "Plant organ" would have a few general characteristics including respiration, input and output of a few substances such as carbohydrate and minerals, weight, and growth, with each characteristic governed by a response rate function. "Leaf" would have additional characteristics such as photosynthetic response, degree of stomatal closure, length, width, thickness, and perhaps angle. If the program code composing each object is carefully written with a clear and well-documented interface to the rest of the program, then the object and its daughter objects should be reusable in different models with little or no change. Then we would have the potential of rapidly building a new model by putting together appropriate objects from other models and adjusting their response rates for various functions such as photosynthesis.

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There are no magic techniques to make model building simple. The actual process of building a model using OOPS techniques would be just about as difficult and expensive as with traditional methods. However, there may be substantial benefits in the development of libraries of reusable modules by adding OOPS to our arsenal of programming techniques. Only a few languages currently support object oriented programming, although OOPS capability is currently being added to additional languages.

For more information on OOPS, including some introductory articles, one may study some of the 1988 and 1989 issues of the monthly journal *Computer Language*. Journals specializing in OOPS will also soon be available.

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Chapter 10

STRUCTURED PROGRAMMING IN SIMULATION MODELS

Evangelyn C. Alocilja, Joe T. Ritchie, and Brian D. Baer

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I. INTRODUCTION

Programming is the process of gaining access to, utilizing, and exploiting the capabilities of a computer through a computer programming language for the purpose of understanding the behavior and performance of a system through a computer simulation model, or for effectively solving computational problems. In plant agriculture, this system could be a maize production system, or the phenology of a crop, or a root growth process, to give a few examples.

Programming is not only an intellectual challenge but an art in itself. According to Dijkstra,[1] it is the art of organizing complexity, mastering multitude, avoiding chaos, and maintaining reliability in a computer program as effectively as possible while providing options for smooth adaptation and modification.

A good simulation model will likely be used by people other than the original programmer. Modification will most certainly be done during the lifetime of the model for many reasons: although logically correct, the model might evoke unsatisfactory computations, or it might turn out to be a perfect solution for not quite the right problem.[1] In this case, there is a need for others to comprehend the organization and logic of the program for the purpose of amendment or verification. But these exercises are difficult if the program is not structured. From personal experience, the authors know that debugging and finding error in an unstructured program is a traumatic task; furthermore, adding a new feature is very difficult.

In today's environment, in which people cost far exceeds machine cost,[2] the maintenance of unstructured programs may not be economical. Thus, in the development of a large crop simulation model, for example, the programmer is required to proceed in a manner that will provide structure and modularity to the program. Existing unstructured models which are frequently used, improved, and modified to suit particular applications, may ultimately be worth the cost and effort involved in structuring the program. In order to make this effort to be less expensive and time-consuming, the structuring may be incorporated during one of the modification processes.

This chapter provides a general overview of the characteristics and advantages of structured programming. It is by no means complete or comprehensive. Those interested in more information will find that a vast amount of knowledge and literature has been amassed on this subject since the early 1970s.

The characteristics described here are those that we followed in structuring the Ritchie soil-water balance model as a component of the CERES-maize crop simulation model. The examples presented are part of that structuring process. The structured Ritchie soil-water balance model would provide a good case study in the application of the structured programming techniques, both because the original model was written as a single module and because the model is frequently used, modified, and improved for various applications.

II. CHARACTERISTICS OF A STRUCTURED PROGRAM

Structured programming is a technique in which rules are applied to the logic of programming by using few, but standardized, control structures. In general, the application of structured programming is known to be successful in (1) reducing test time, (2) increasing programmer productivity, (3) producing clear and comprehensible solutions, and (4) increasing reliability and maintainability of programs.[2-4] The reason for the reduced test time and programmer productivity is that a structured code is readable and can be tested by module, and errors therefore are easily identified. Because structured programs are loosely coupled and highly modularized, there is a better chance that other parts of the program will be unaffected when the code is changed in one part, thus increasing reliability and maintainability.

The desirability of these features cannot be overemphasized. According to Weinberg,[2] developmental testing, maintenance, and enhancement of programs consume at least 75% of

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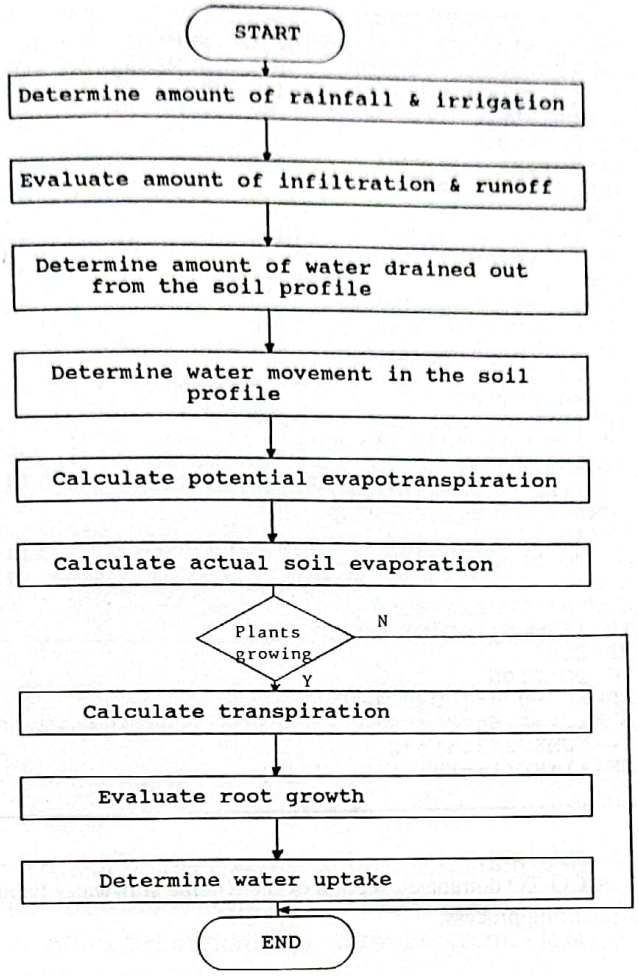

FIGURE 1. A flowchart of the structured Ritchie soil-water balance model.

overall systems cost; systems should therefore be designed so that they can be easily debugged and maintained.

A good structured program includes the following characteristics: (1) it has a top-down design, (2) it is modular, (3) it has GO-TO-less, (4) it is highly cohesive, and (5) it is loosely coupled.

A. TOP-DOWN DESIGN

"Half the battle is won" when the development of a program is based on a good design. According to Swann,[4] reliability and modifiability cannot be programmed into a bad design. Structured, top-down design starts with a broad definition of the task and works down to the details of subtasks, resulting in a hierarchy of functional modules.[2,4] Each module is designed to be as independent as possible from every other one, so that all of the elements in a module contribute to only a single function. Figure 1 illustrates a top-down design of the structured Ritchie soil-water balance model.

During the design of the program, it is a good practice to decide on the approximate length of code for each module, in order to produce a program that is comprehensible, readable, modifiable, and reliable. Generally, a module design that fits on one page of $8\,{}^{1}/_{2} \times 11$ in. paper is a good scale. However, it is not good to split a module arbitrarily for the sake of maintaining length, which is only one general guideline. During the design process, a logical, sequential, and functional relationship in each module should be maintained.

During the testing phase of the program, each module is tested separately. This allows for quick error detection and thus saves time and effort.

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```
      IF (SUMES1.GE.U.AND.PINF.GE.SUMES2) GO TO 1400
      IF (SUMES1.GE.U.AND.PINF.LT.SUMES2) GO TO 1500
      IF (PINF.GE.SUMES1) GO TO 1800
      SUMES1=SUMES1-PINF
      GO TO 1900
1400  PINF=PINF-SUMES2
      SUMES1=U-PINF
      T=0.
      IF (PINF.GT.U) GO TO 1800
      GO TO 1900
1500  T=T+1.
      ES=3.5*T**0.5-SUMES2
      IF (PINF.GT.0.) GO TO 1600
      IF (ES.GT.EOS) ES=EOS
      GO TO 1700
1600  ESX=0.8*PINF
      IF (ESX.LE.ES) ESX=ES+PINF
      IF (ESX.GT.EOS) ESX=EOS
      ES=ESX
1700  CONTINUE
      SUMES2=SUMES2+ES-PINF
      T=(SUMES2/3.5)**2
      GO TO 2100
1800  SUMES1=0.
1900  SUMES1=SUMES1+EOS
      IF (SUMES1.GT.U) GO TO 2000
      ES=EOS
      GO TO 2100
2000  ES=EOS-0.4*(SUMES1-U)
      SUMES2=0.6*(SUMES1-U)
      T=(SUMES2/3.5)**2
2100  SW(1)=SW(1)-ES*.1/DLAYR(1)
```

FIGURE 2. A GO-TO dominated section of the Ritchie soil-water balance model before the structuring process.

B. MODULAR

A module is a section of program code, sometimes called a subroutine, which performs well-defined, independent sets of operation or logical function.[4,5] A module is called on to perform a process independent from other modules. A module controls itself and all of the subordinate modules — that is, in a tree structure, the top module controls the entire structure and determines when the other modules below it will be executed.[4] Control is passed back to the calling module when the execution is complete. Each module has only one entry point for the input and one exit point for the output.

As noted earlier, the original version of the Ritchie soil-water balance model was a single subroutine of the CERES-maize crop simulation model. The soil-water balance model has been structured into the following modules: irrigation, runoff, drainage, water movement in the soil profile, potential evapotranspiration, actual soil evaporation, plant transpiration, root growth, and water uptake by the plant, as illustrated in Figure 1. This modularization allows disciplinary specialists to improve each module without having to learn in detail the functions of the other modules. For example, a root growth specialist can study and improve the root growth module without having to sort through the complexities of the other modules. In fact, improvements on multiple modules can proceed independent of, and simultaneous with, each other.

C. GO-TO-LESS

A major indicator of an unstructured program is the overuse of the GO-TO statement. According to Liffick,[5] there are several advantages to eliminating the GO-TO statement: (1) it will help provide structure to the program; (2) the program will become more efficient (the branching due to the GO-TO statement require significant amounts of computer time but they perform no real work); (3) it is easier to isolate and correct errors and thus reduce the maintenance effort; and (4) the program becomes highly readable, thus facilitating the addition

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```
IF ((SUMES1 .GE. U) .AND. (PINF .GE. SUMES2)) THEN
    PINF = PINF-SUMES2
    SUMES1 = U-PINF
    T=0.0
    IF (PINF .GT. U) THEN
       SUMES1 = 0.0
    ENDIF
    CALL ESUP(EOS,ES,SUMES1,SUMES2,T,U)
ELSE IF ((SUMES1.GE.U) .AND. (PINF.LT.SUMES2)) THEN
    T = T+1.0
    ES = 3.5*T**0.5-SUMES2
    IF (PINF .GT. 0.) THEN
       ES = AMIN1(EOS,(0.8*PINF),(ES+PINF))
    ENDIF
    SUMES2 = SUMES2+ES-PINF
    T = (SUMES2/3.5)**2
 ELSE IF (PINF.GE.SUMES1) THEN
    SUMES1 = 0.0
    CALL ESUP(EOS,ES,SUMES1,SUMES2,T,U)
 ELSE
    SUMES1=SUMES1-PINF
    CALL ESUP(EOS,ES,SUMES1,SUMES2,T,U)
 ENDIF
 SW(1) = SW(1)-ES*0.1/DLAYR(1)
```

FIGURE 3. A GO-TO-less structured Ritchie soil-water balance model equivalent to Figure 2.

of new features. Figure 2 illustrates a GO-TO dominated section of the soil-water balance before the structuring effort. The GO-TO statements produced a "spaghetti" type of structure in which it is nearly impossible to follow the logical flow of the program. Figure 3 shows the GO-TO-less, structured equivalent of Figure 2.

However, while indiscriminate use is discouraged, there are cases when a wise use of a GO-TO statement can make the logic more understandable.[4] In fact, in some computer programming languages (as in most implementations of FORTRAN and BASIC), it is impossible to avoid the use of GO-TO statements altogether, because these programming languages lack some of the more complex data structures. The programmer should carefully decide when to use a GO-TO statement.

D. HIGHLY COHESIVE

A cohesive, structured module performs one complete, independent function.[4] It has minimum branching. Cohesiveness can be achieved by putting together statements and functions that are logically and functionally related. In order to maintain high cohesiveness, programmers must avoid putting code into unrelated modules simply because it happens to be convenient at the time. This requires a strict discipline on the part of the programmer, especially during the program development phase. Cohesiveness has been much improved in the structured Ritchie soil-water balance model.

E. LOOSELY COUPLED

Another characteristic of a structured program is that the modules are loosely coupled. According to Swann,[4] "the greatest cost savings are achieved when modules can be understood and solved independently of any other module in the structure." The use of flags or switches to communicate between modules will cause dependency and coupling between modules. This mechanism is a likely source of bugs and should therefore be avoided as much as possible. Loosely coupled modules prevent what Weinberg[2] calls as the "ripple effect", in which a change in one module causes a bug in another module.

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```
ET = ES + EP
CEP = CEP + EP
CET = CET + EP
CRAIN = CRAIN + PRECIP
```

FIGURE 4. An example of a sequence control structure, in FORTRAN code, from the main program of the structured Ritchie soil-water balance model.

```
IF (LAI .LE. 3.0) THEN
   EP = EO*(1.0-EXP(-LAI))
ELSE
   EP = EO
END IF
```

FIGURE 5. An example of an IF-THEN-ELSE control structure, in FORTRAN code, from the plant transpiration module of the structured Ritchie soil-water balance model.

III. CONTROL STRUCTURES IN STRUCTURED PROGRAMMING

Swann[4] presented four basic control structures generally used in structured programming: sequence, IF-THEN-ELSE, DO-WHILE, and DO-UNTIL. All other control structures can be treated as combinations or modifications of these four structures.

The programmer must be familiar with the programming language being used in order to implement these structures correctly. The control structures discussed in this section are illustrated with the use of the structured Ritchie soil-water balance model in FORTRAN code.

A. SEQUENCE

The sequence control structure is the simplest and most fundamental of all the structures. It is a structure in which one statement is executed after another for all conditions. Branching occurs only when the logic calls for a module or subroutine. An example of a sequence structure from the main program of the structured Ritchie soil-water balance model, in FORTRAN code, is illustrated in Figure 4.

B. IF-THEN-ELSE

The IF-THEN-ELSE control structure is a simple binary test: when a certain condition is true, a function is executed; when the condition is false, another function is executed. These structures can be strung together to test whether a variable is at one of a number of possible states. The CASE statement in Pascal and the SWITCH statement in C provide a more eloquent way to perform these multiple IF-THEN-ELSE structures. An example of a simple IF-THEN-ELSE structure from the plant transpiration module of the structured Ritchie soil-water balance model, in FORTRAN code, is shown in Figure 5.

C. DO-WHILE

The DO-WHILE control structure is a top-tested structure and provides for looping. At the beginning of the section of the code, a test is made to determine whether the body of the loop is to be executed. If the test is true, the loop is executed. After execution, control returns to the

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```
C *** Begin DO-WHILE [RLV(L) is not equal to 0 and
C       L is less than or equal to NLAYR] ********

3400   IF ((RLV(L) .NE. 0.) .AND. (L .LE. NLAYR)) THEN
                .
                .
                .
          TRWU = TRWU + RWU(L)
          L = L + 1
          GO TO 3400
        END IF
C *** End DO-WHILE Loop
```

FIGURE 6. An example of a DO-WHILE control structure, in FORTRAN code, from the water uptake module of the structured Ritchie soil-water balance model.

```
C * Begin DO-UNTIL [CUMDEP is greater than RTDEP
C     or L is greater than NLAYR] *******

30   L = L + 1
               .
               .
               .
     RLDF(L) = AMIN1(SWDF,RNFAC)*WR(L)*DLAYR(L)
     SWDF3=SWDF3+(SW(L)-LL(L))/(DUL(L)-LL(L))*DLAYR(L)
     IF ((CUMDEP.LT.RTDEP) .AND. (L.LT.NLAYR)) THEN
       GO TO 30
     END IF
C * END DO-UNTIL Loop
```

FIGURE 7. An example of a DO-UNTIL control structure, in FORTRAN code, from the root growth module of the structured Ritchie soil-water balance model.

test statement preceding the loop body and the test is repeated. The loop is executed again as long as the test is true. When the test is false, the loop body is skipped and control goes to the next structure in the sequence. Examples of DO-WHILE structures are the Pascal WHILE-DO loop and the C WHILE loop. The FORTRAN DO loop, the Pascal FOR-DO, and the C FOR loop are special cases of the DO-WHILE structure. The programmer selects a beginning and ending value and an increment; the languages automatically increment the beginning value during each pass through the loop while the new value has not reached the ending value. The loop terminates when the ending value is reached. Figure 6 provides an example of a DO-WHILE loop implemented in FORTRAN from the water uptake module of the structured Ritchie soil-water balance model.

D. DO-UNTIL

The DO-UNTIL control structure is a bottom-tested structure and provides another structure for looping. The body of the loop is executed first and then a test is made to determine whether the loop should be repeated. If the test is false, the loop body is executed again. This process continues until the test is true, after which the control goes to the next structure in the sequence. This control structure differs slightly from the DO-WHILE. The DO-UNTIL causes the body of the loop in the structure to be executed at least once, while in the DO-WHILE, the function may not get executed at all. The REPEAT-UNTIL loop in Pascal is an example of the DO-UNTIL structure. The FOR-NEXT loop in BASIC is a special case of the DO-UNTIL structure, in which the program automatically increments a value for each cycle of a loop until that value reaches an ending value. Figure 7 shows a DO-UNTIL structure in FORTRAN code from the root growth module of the structured Ritchie soil-water balance model.

In addition to the use of these control structures when coding a program, the following

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practices are helpful: (1) use indentation to show blocks created from control structures; (2) provide comments to explain each module and any complex logic or operation; and (3) use meaningful variable and module names. The use of these techniques will make a program easier to maintain and modify.

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Chapter 11

PREDICTING MAIZE PHENOLOGY

J. R. Kiniry and R. Bonhomme

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Models of development and grain yield of maize (*Zea mays* L.) have become numerous due to the wide distribution of the species and its vulnerability to climate stress. Models of maize production include the Runge-Benci model,[1] the Splinter model,[2] SIMAIZ,[3] the "Bio-photothermal" model,[4] the "Energy-Crop Growth" model,[5] CORNF,[6] and CERES-Maize.[7]

Most maize models are designed to predict the response of grain yield to environment, but they differ in terms of the type and complexity of biological processes included. These differences are especially evident in their techniques of predicting phenology. The Runge-Benci model makes no attempt at predicting development. Both the Splinter model and SIMAIZ both predict growth stages by accumulating degree days. When the sum reaches a specified value, the plant is assumed to be at the next stage. No attempt is made to quantify photoperiod sensitivity. The "Energy-Crop Growth" model also predicts phenology based solely on temperature. The temperature function is a series of four lines fit to growth-rate data. The "biophotothermal" model sums genetic, photoperiodic, and thermal factors in order to predict the number of days to tassel initiation. CORNF and CERES-Maize each use photoperiod and temperature to predict development. In both, photoperiods greater than 12.5 h delay tassel initiation in sensitive genotypes and increase the final number of leaves. However, CERES-Maize provides a more detailed system of predicting stages and number of leaves, and its components can be more easily tested and validated. Recently, a phenology model which includes leaf initiation, leaf collar appearance, and developmental stages similar to CERES-Maize was described in Japan.[8,9] In this model, development rates are temperature dependent and photoperiod sensitivity is ignored.

The objective of this chapter is to describe a model for predicting maize phenology based on photoperiod and temperature. Tassel initiation and leaf primordia initiation are simulated to predict total number of leaves (TLNO). Rate of leaf tip appearance is simulated to predict when the last leaf will emerge, and soon thereafter silking is predicted to occur. Three phases between silking and physiological maturity are simulated. Two processes involved in phenology which are not included are the dependence of seed germination on soil water and the dependence of physiological maturity on assimilate supply. By omitting these, both a soil water balance section and an assimilate allocation section could be omitted.

Assumptions, experimental justification, and possible sources of errors are discussed for the simulated processes. Tests of the predictive ability of the model for silking date and final number of leaves are also included. Finally, areas for future research related to this model are described.

I. GENERAL MODEL DESCRIPTION

The model was written in FORTRAN and requires approximately 3 s of computer time for one season on a large mainframe computer. Simulations involving several years of weather data can be run with the same cultivar and planting date. Required input data are latitude (LAT), day of the year of sowing (ISOW), daily minimum and maximum air temperatures (TEMPMN and TEMPMX), and three cultivar-specific parameters, P1, P2, and P5. The three parameters can be independently derived as described in the text or can be estimated from values of similar cultivars.

There are nine phenological phases or stages including one for the fallow period after harvest and before planting. The system of numbering the stages is circular with an identifying integer (ISTAGE) for each (Table 1).

The model has a daily incrementing loop which executes until the end of the weather data is reached (Figure 1). Daily temperatures are read first. Next, pertinent variables are calculated. Finally, the decision is made concerning whether the next phenological stage has been reached.

Basic assumptions relate to the development rate response to temperature and to photoperiod. The model assumes rate of development increases linearly above a base temperature up to 34°C and then linearly decreases to 0 from 34 to 44°C. These rates include development from germination to seedling emergence, development in the juvenile phase, leaf initiation and leaf tip appearance, and development from silking to physiological maturity. Rate of photoperiodic

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TABLE 1
Description of the Phenological Phases Used in the Model

7	Prior to sowing (fallow)
8	Sowing to germination (1 d)
9	Germination to seedling emergence
1	Seedling emergence to end of juvenile phase
2	End of juvenile phase to tassel initiation (photoperiod sensitive phase)
3	Tassel initiation to silking
4	Silking to beginning of effective filling period of grain (lag phase)
5	Effective filling period of grain
6	End of effective filling period to physiological maturity (black layer)

induction is assumed to decrease with increasing photoperiod for photoperiods greater than 12.5 h. The number of days of delay in tassel initiation per hour increase in photoperiod is assumed to be a constant for any given photoperiod-sensitive cultivar.

A. TEMPERATURE-DEPENDENT RATES

Rates of development from germination to seedling emergence, from seedling emergence to end of the juvenile phase, from silking to maturity, and rates of leaf initiation and leaf tip appearance are all simulated using a growing degree day (GDD) or daily thermal time (DTT) system. The base temperature is 8°C for all these processes except seedling emergence, with a base of 10°C. As noted, development rate is assumed to decrease to 0 as temperature increases from 34 to 44°C. When TEMPMN and TEMPMX encompass the base temperature, or 34°C, intermediate values are calculated with a zero-to-one factor (TMFAC) calculated with a polynomial fit to a sine wave curve. The interpolated values are then used to calculate the daily value for DTT.

Rate of coleoptile elongation linearly increases from a value near 0 at 10°C.[10] Allowing 1 d for germination when adequate soil moisture is present, seedling emergence requires an average of 45 DTT_{10} when the planting depth is 5.0 cm.[11]

Two leaf developmental processes, primordia initiation and tip appearance, allow for prediction of TLNO and prediction of tassel emergence date. Both number of primordia initiated and number of tips visible outside the whorl are linear as a function of time in constant temperature growth chambers or as a function of cumulative DTT_8 in the field. This linearity in initiation was shown in growth chambers by Warrington and Kanemasu[12] and in the field by Kiniry and Ritchie[13] (Figure 2). Likewise, tip appearance rate is constant after the second leaf in growth chambers (Figure 3) and as a function of cumulative DTT in the field.[14] It is interesting to note that number of days from tip appearance to collar appearance as a function of leaf number is nonlinear (Figure 4). Stem elongation causes the last few leaf collars to come out more quickly than the earlier ones. This is why the DTT between leaf collars vary with leaf number[14] and why modeling phenology based on number of leaf collars is more difficult than with leaf tips.

The response rate of leaf tip appearance to temperature (Figure 5)[13,15] is the basis for the DTT system discussed previously. A similar response was demonstrated by Chirkov.[16] Rate increases linearly from 8 to 34°C and then decreases to 0 at 44°C. A similar base temperature for leaf initiation rate can be derived using results of Warrington and Kanemasu[12] (Figure 6).

Likewise, rates of development to tassel initiation and to anthesis or silking have a base temperature near 8°C. Warrington and Kanemasu[17] found rate of development to tassel initiation had a base temperature of 8.4°C for one hybrid and 7.8°C for another. Field results of Durand et al.[18] support use of a base temperature of 7°C rather than the traditional 10°C for rate of development toward silking.

Development in the anthesis or silking to maturity interval can also be shown to have a base

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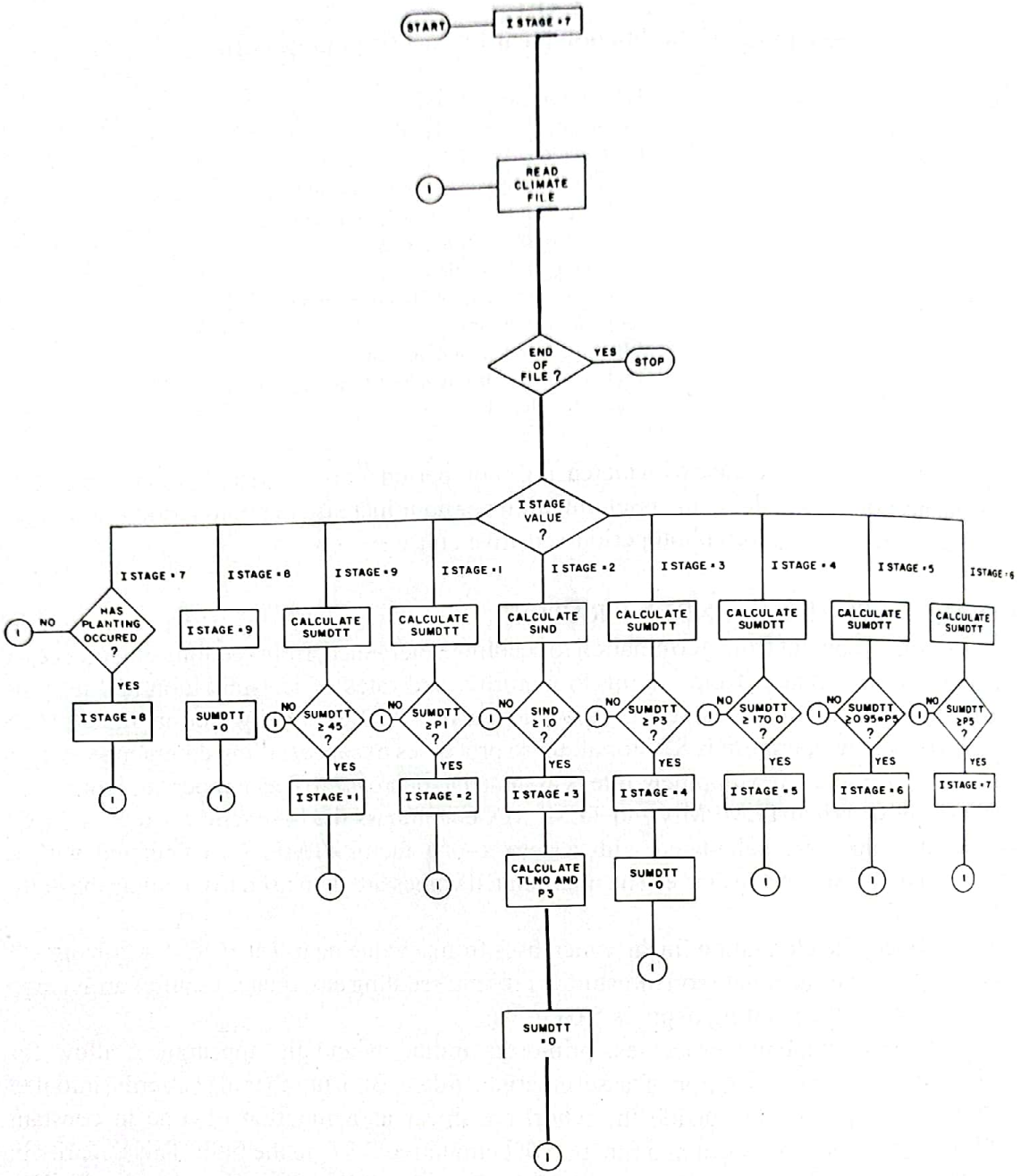

FIGURE 1. A flow diagram of the maize phenology model.

temperature near 8°C. With the admittedly scant data of Badu-Apraku et al.,[19] the base temperature for development rate of maize is 8.2°C (Figure 7). With similar data for sorghum (*Sorghum bicolor* L. Moench)[20] with treatments of 15, 22.5, and 30°C, a fitted exponential equation forced through the x-intercept of 5°C fell very close to a response line with an 8°C base temperature (Figure 8).

B. PHOTOPERIODIC INDUCTION

Photoperiod is assumed to directly affect only date of tassel initiation.[21] From seedling emergence until the start of the photoperiod-sensitive phase, a cultivar-specific sum (P1) (Table 2) of DTT_8 are accumulated during the photoperiod-insensitive juvenile phase. All cultivars are assumed to reach tassel initiation 4 d after the end of the juvenile period if photoperiods are 12.5 h or less. In longer photoperiods, tassel initiation is delayed according to a cultivar-specific value of sensitivity (P2) in units of days of delay per hour increase in photoperiod.[22,23] Duration of the

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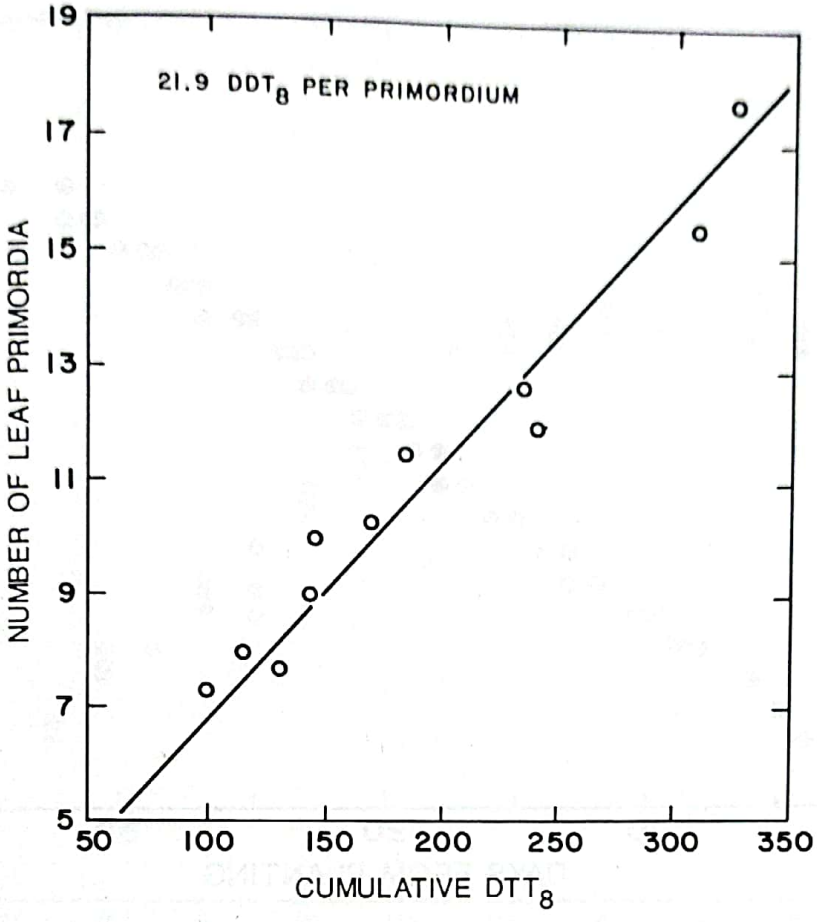

FIGURE 2. Number of leaf primordia as a function of cumulative DTT_8 for a 1981 sowing at Temple, TX of maize hybrid B73 × Mo17.[13]

photoperiod-sensitive phase is assumed to be independent of temperature. Delay in tassel initiation due to long photoperiods causes an increased number of leaf primordia to be initiated, thus increasing the number of leaf tips which must emerge before tasseling and delaying tasseling and silking.

C. PREDICTION OF DTT-8 FOR TASSEL EMERGENCE

Since leaf initiation rate, leaf tip appearance rate, and rate of development to tassel initiation and anthesis all use the same DTT_8 system, the DTT_8 from seedling emergence to tassel initiation can be directly related to the DTT_8 from seedling emergence to tassel emergence. Likewise, the number of leaf tips visible at tassel initiation can be directly related to the TLNO produced.

The relationship between DTT_8 from seedling emergence to tassel emergence and to tassel initiation showed that for each DTT_8 unit tassel emergence is delayed, tassel initiation was delayed 0.46 units.[23] Analysis of similar data for 6 maize cultivars grown in 2 photoperiods at 24°C gave a value of 0.47 units.[24] Assuming the DTT_8 per leaf tip is constant after the first two leaves, a similar relationship should be true for the TLNO and the number of leaf tips visible at tassel initiation (TILNO). Three independent projects have shown this to be true. Russell,[25] working with a wide range of genotypes in a wide range of field environments, found:

$$TILNO = 0.44 * TLNO - 2.30$$

Similarly, Inoue[26] found the relationship to be

$$TILNO = 0.42 * TLNO - 2.2$$

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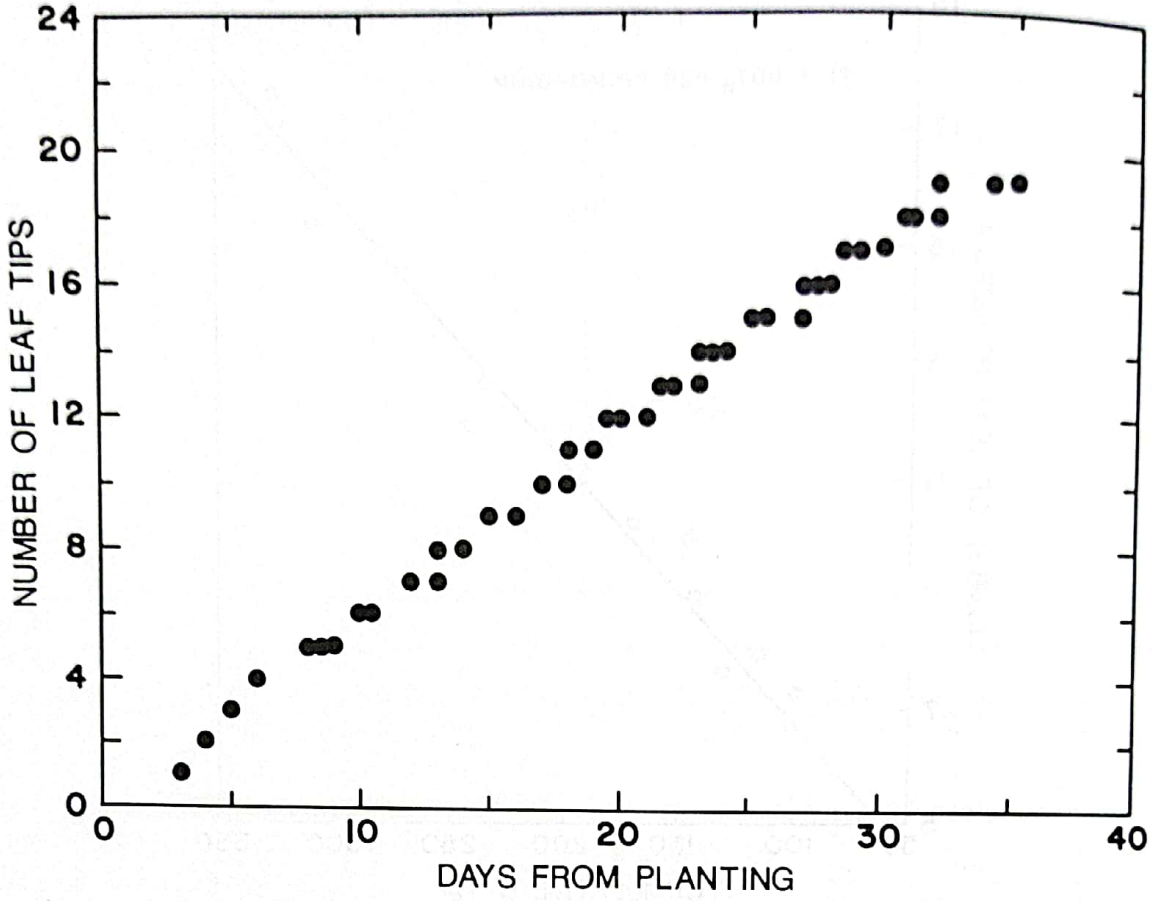

FIGURE 3. Number of leaf tips emerged as a function of days from sowing for maize hybrid Mo17 × A634 in the Duke University Phytotron at 25°C.[40]

Using data with short season hybrids,[27] the relationship was: TILNO = 0.44 * TLNO – 1.95. The slope value can be thought of as representing the ratio of the DTT_8 per leaf primordium to the DTT_8 per leaf tip. For the present model, we assumed 18 DTT_8 per primordium and 39 DTT_8 per leaf tip for a ratio of 0.46. The x-intercept, 5.2 leaves for the first two equations and 4.4 for the last one, is similar to the 6 leaf primordia present at seedling emergence.[12,13]

D. DTT-8 PER LEAF PRIMORDIA AND PER LEAF TIP

Consistency in the DTT_8 per leaf primordium or tip is vital for accuracy of the present model. Environmental alteration of the values or differences between cultivars in the values need to be identified and quantified before the model will make consistently accurate predictions.

A field experiment sown in March in Temple, TX, demonstrated that there were 21 DTT_8 per leaf primordium (Figure 2).[13] Results in a growth chamber showed values of 19 to 21 DTT_8 per primordium.[12] The mean value for a number of cultivars grown in the field in Japan was 17 DTT_{10} per primordium.[9] Assuming 2 d per primordia, this would be 21 DTT_8 per primordium.

However, in spite of this apparent stability in DTT_8 per primordium, there appears to be some variability between genotypes. While a fall sowing of three cultivars of drastically different maturity failed to show difference in initiation rate,[11] Torigoe et al.[9] found extremes of 15.3 and 20.0 DTT_{10} per primordium. In addition, the fall sowing had 29 DTT_8 per primordium, the cause of which has not yet been determined.

Leaf tip appearance requires 36 to 40 DTT_8 per leaf in many temperate environments. Analysis of data from four sources (Figure 9) indicated that there were 36 DTT_8 per leaf tip. As noted previously, the model assumes that there are 39 DTT_8 per leaf tip after the second leaf. Variability in this value may arise due to genotypic differences or differences between the tropical and temperate environments. Tollenaar et al.[28] reported differences as great as 16% of

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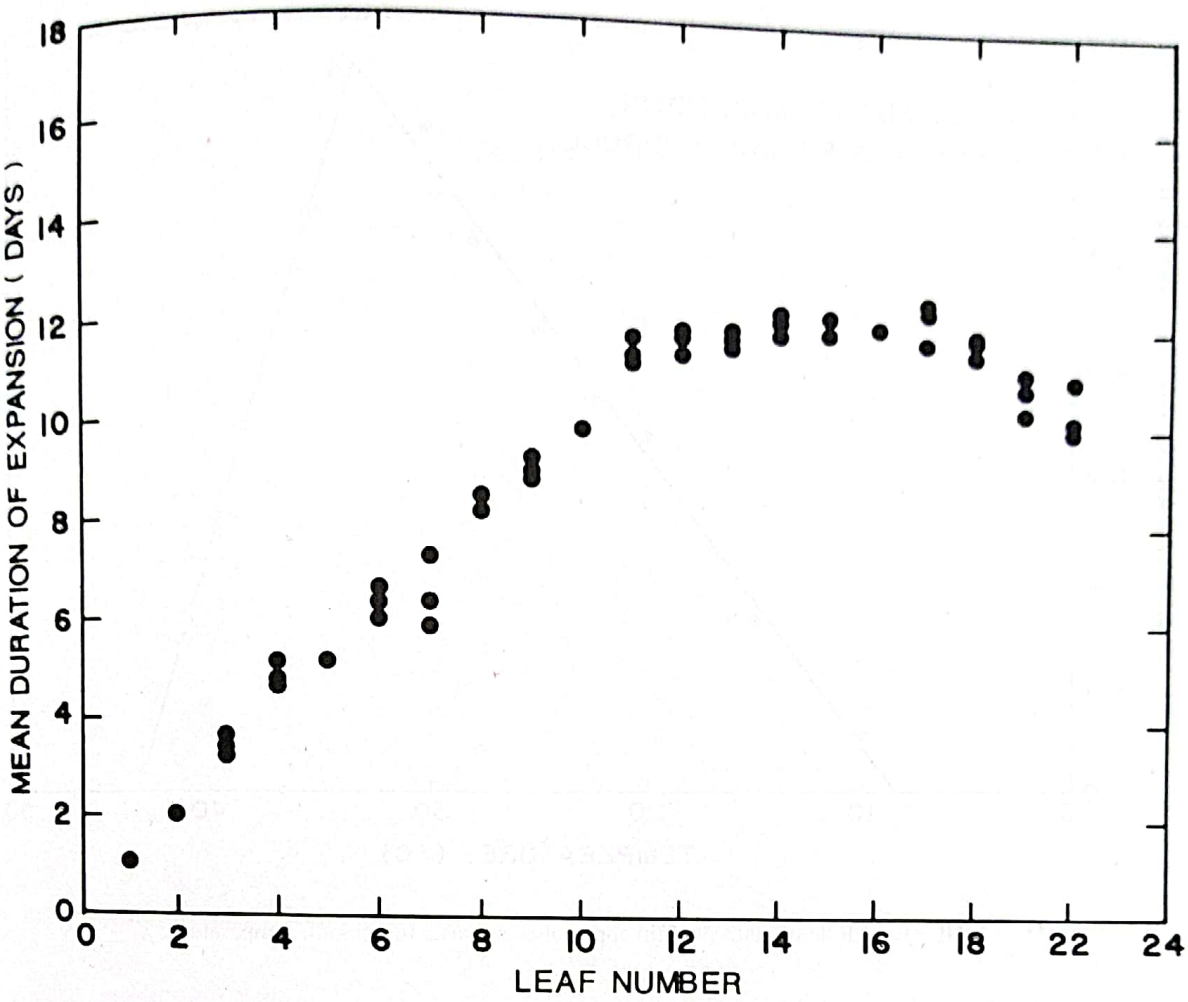

FIGURE 4. Duration of leaf expansion as a function of leaf number for maize hybrid Mo17 × A634 in the Duke University Phytotron at 25°C.[40]

the mean in the DTT required per leaf tip. Similarly, in a field planting at Temple, TX[11] the mean was 37.5 DTT_8 per leaf tip, while values for different hybrids ranged from 34 to 41 DTT_8 (Figure 10). Further attempts at finding maize cultivars with different temperature responses[11] consisted of using one inbred, Z7, which was reported as having high growth rates in cool temperatures,[29] and two races from Mexico, Sinaloa and Amarillo Salvadoreno, which showed promise of having unusual temperature responses.[30] Of the cultivars sown at Temple in 1984, only Z7 had a significantly different rate of leaf tip appearance relative to the commercial hybrid Pioneer 3780 (Figure 11). Plants of the inbred Z7 were weak and not competitive, so even its differences in development could be questioned.

Values for DTT_8 per leaf tip can be 30% greater in tropical areas than in temperate ones. Leaf appearance for 5 sowing dates of 4 cultivars in the Caribbean basin required an average of 50 DTT_8 per leaf tip.[31] Future research into causes of such deviations will help to make the present model more general.

E. THE GRAIN FILLING PERIOD

Three intervals[32] in the silking to physiological maturity (black layer) period are simulated. These phases are a lag phase, a period of nearly linear grain filling called the effective fill period, and the period from the end of the effective fill period to physiological maturity.

Summed DTT_{10} has been shown to be less variable than days for the interval between silking and physiological maturity for different planting dates.[33] As discussed previously, the rate of development from silking to maturity in the present model uses a base temperature of 8°C. The model assumes a cultivar-specific sum of DTT_8 from silking to maturity.

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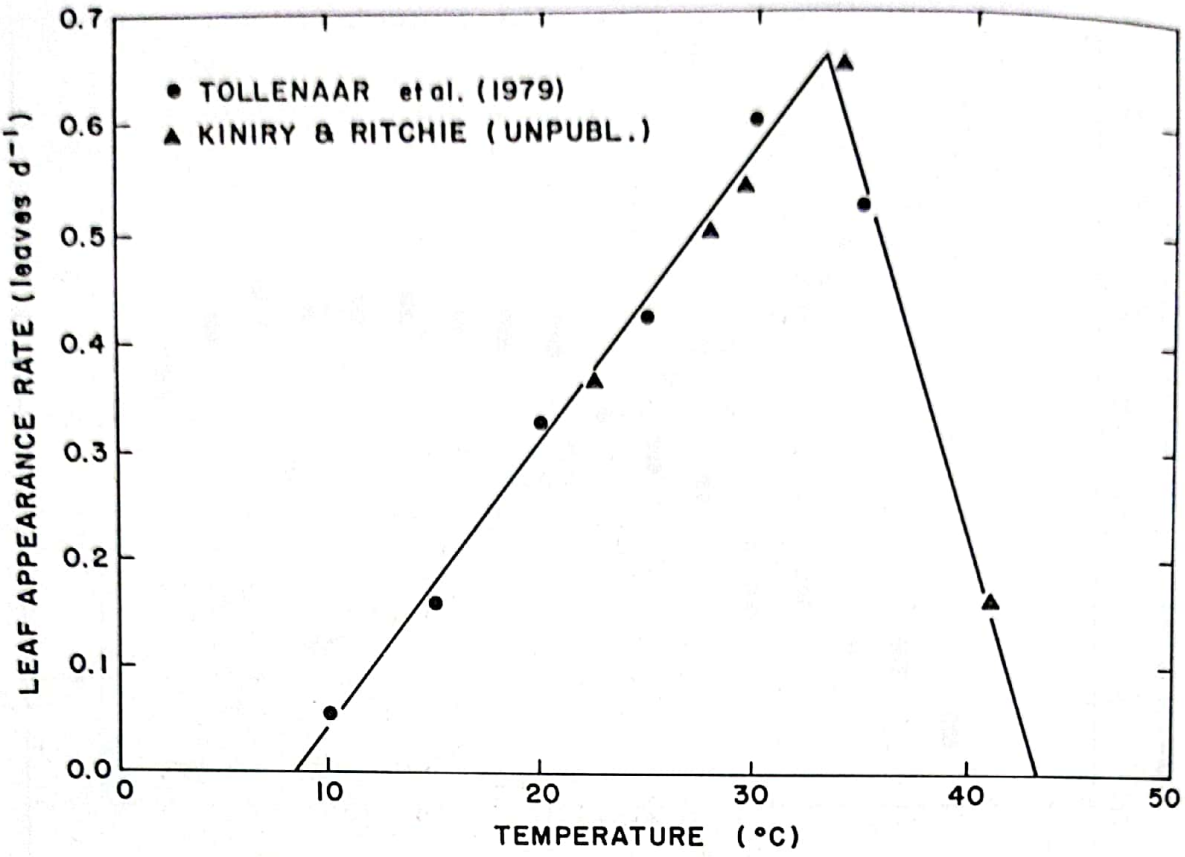

FIGURE 5. Rate of maize leaf tip appearance rate as a function of temperature.

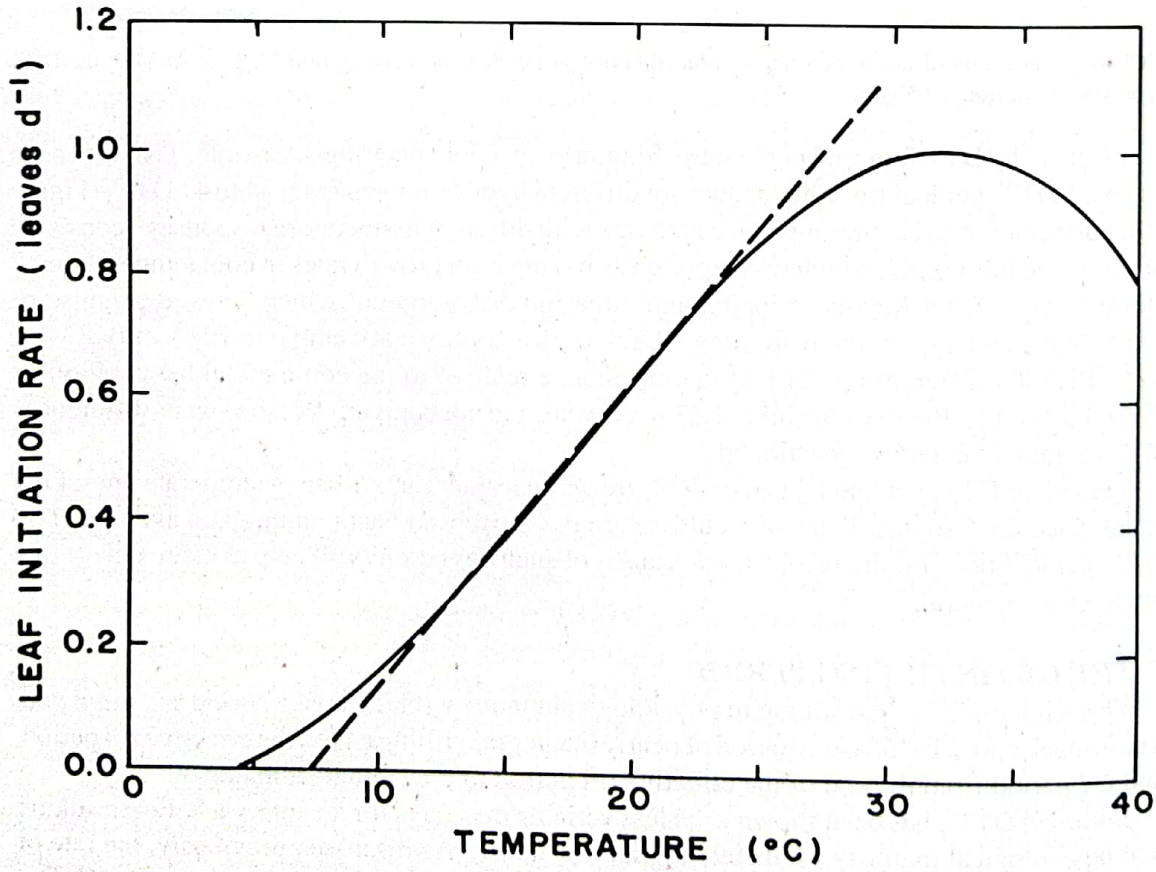

FIGURE 6. Rate of maize leaf initiation rate as a function of temperature. The solid line represents a function derived by Warrington and Kanemasu.[12]

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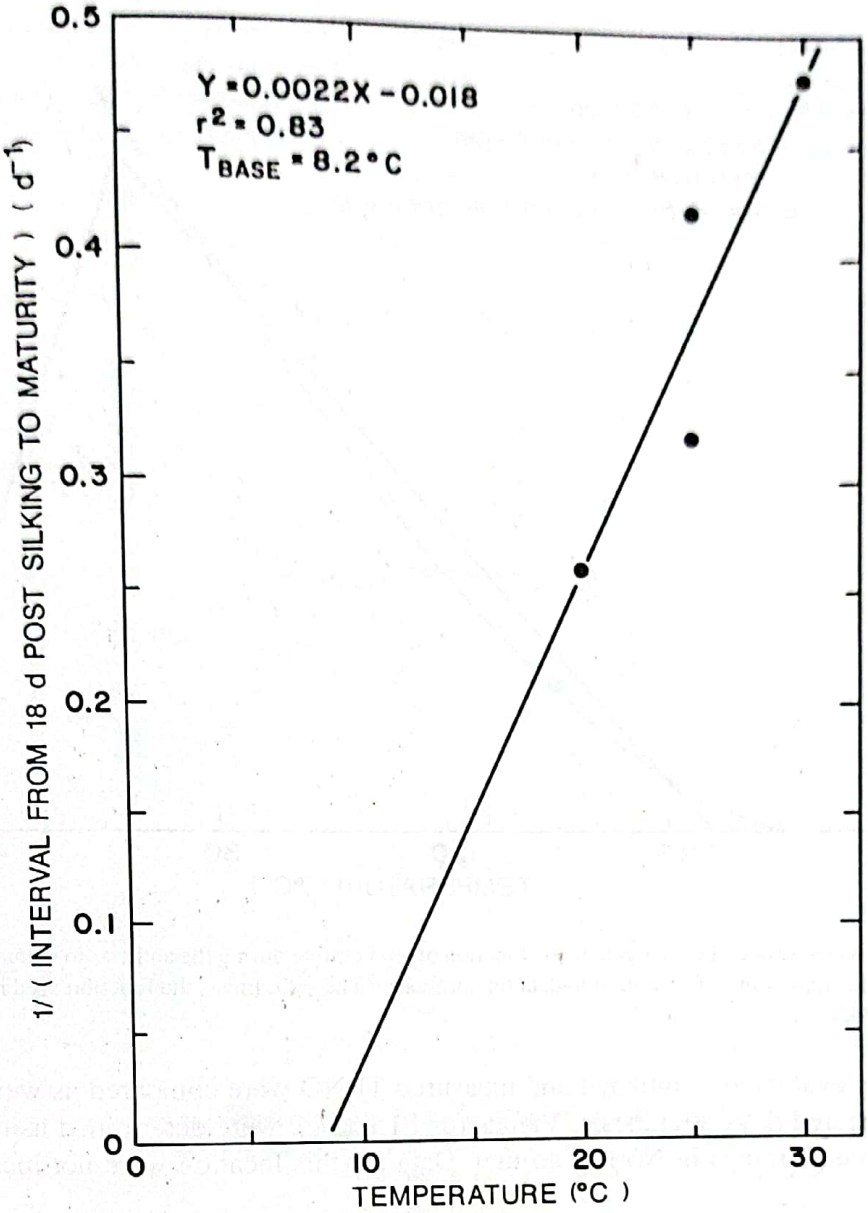

FIGURE 7. Development rate as a function of temperature during the silking to maturity interval of maize. Derived from data of Badu-Apraku et al.[19]

The DTT for the lag phase has been shown to not differ significantly between cultivars.[34] In the present model, this was determined to be 170 DTT_8.[35] The effective fill period begins at the end of the lag phase and ends when 95% of the total DTT_8 from silking to physiological maturity have been accumulated. The last developmental phase, from the end of the effective fill period to physiological maturity, requires the last 5%. A statement was added to the model to prevent delayed maturity if cool temperatures prevent DTT accumulation during this last, short stage. If the DTT is 2.0 or less on a day during this last stage, maturity is assumed to occur.

Values for P5, the required sum of DTT_8 from silking to maturity, ranged from 665 for B14 × OH43 to 940 for Pio x304C (Table 2). These values were derived from field data with dates of silking and maturity measured.

II. TEST RESULTS

Test results will be confined to the TLNO produced and days to anthesis (measured pollen shed and simulated silking). Tests were conducted on an independent data set from Russell.[25] A long season, photoperiod sensitive inbred, Tx601, and an intermediate maturity hybrid, L36

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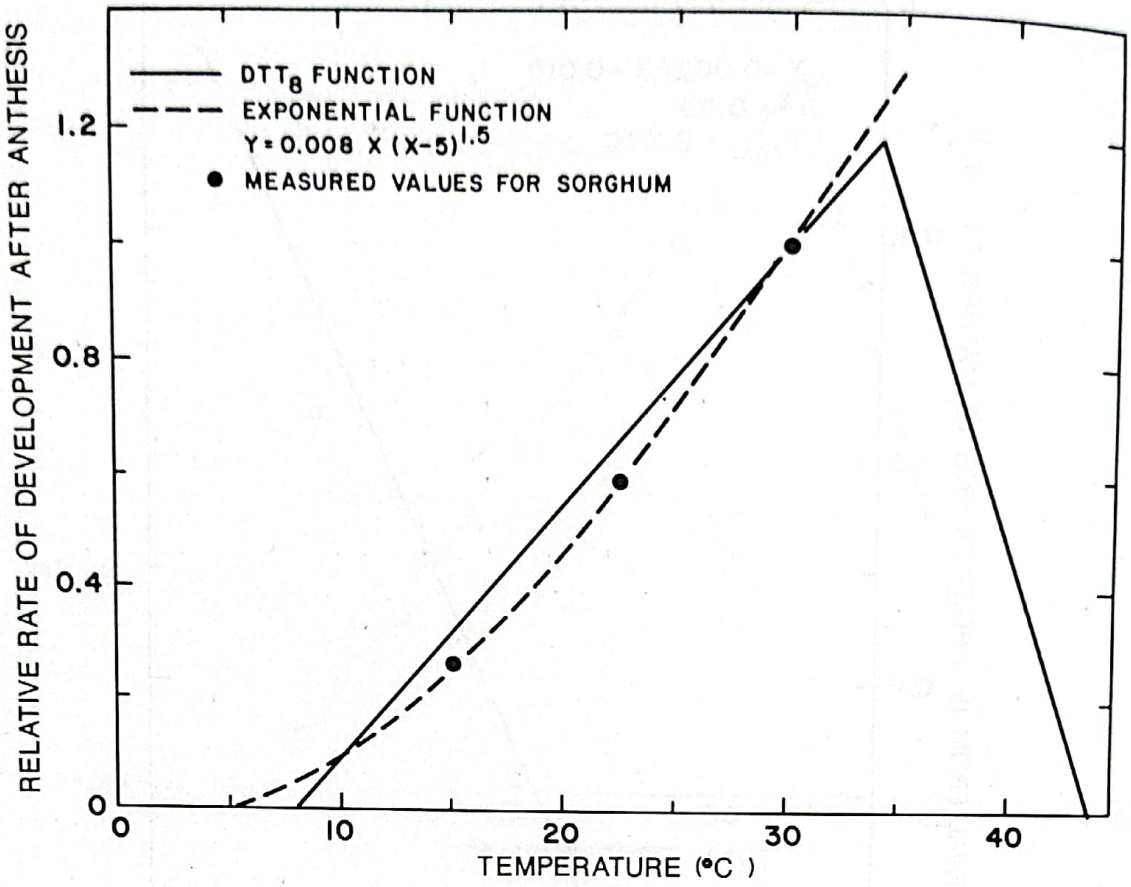

FIGURE 8. Relative rate of development as a function of temperature during the anthesis to maturity interval. The dashed line represents a function fit to data for sorghum.[20] The solid line is the function used in the maize phenology model.

× B14A, were evaluated. Simulated and measured TLNO were compared as were simulated days and measured days to anthesis. Values for P1 and P2 were determined using measured values for three plantings in North Carolina. Data for this location were not included in the evaluation.

Simulated TLNO was never greater than three leaves different from measured for either the hybrid or the inbred (Tables 3 and 4). The mean errors were 0 and 1, respectively, for the cultivars. In both cases the standard deviation was 2. There was no tendency for the greatest errors to be in the warmer or cooler environments. Likewise, in contrast to findings of Bonhomme et al.,[36] errors showed no obvious relationship to temperature near tassel initiation (Tables 3 and 4). The three largest negative errors were in California, Iowa, and South Dakota. The value from Hawaii was one of the two with the largest positive error. However errors in the similarly warm Florida location were never greater than 1.

The small range of variability in TLNO for the hybrid was not explained by the simulated values, but the model simulations accounted for much of the variability in TLNO of Tx601. The r-squares for the regression of measured TLNO as a function of simulated TLNO had values of 0.18 for the hybrid (not shown) and 0.54 for Tx601 (Figure 12). The slope for Tx601 was 0.77, fairly close to the ideal value of 1.0.

The model did a better job of accounting for differences in days to anthesis than for differences in TLNO. Regressions of measured days to pollen shed on simulated days to silking had slopes of 0.80 and 0.77 and values for r-square of 0.76 and 0.68 (Figure 13). For both cultivars the regression lines were close to the 1:1 line. There were three data sets for L36 × B14 and two with Tx601 with errors of 10 d or greater (Tables 3 and 4). The means of the errors were 2 and -1 and the values for South Dakota were 6 and 7. As was the case with predictions of TLNO, there was no apparent trend for the greatest errors to occur at the most northern or southern locations.

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TABLE 2
Genotype-Specific Values for the DTT_8 from Seedling Emergence to the End of the Juvenile Phase (P1): The Days Delay in Tassel Initiation for Each Hour Increase in Photoperiod (P2), and the DTT_8 from Silking to Physiological Maturity (P5)

Cultivar	P1 DTT_8	P2 dh^{-1}	P5 DTT_8
Southern Canada			
CORNL281	110	0.30	—
CP170	120	0.00	680+
F7 × F2	125	0.00	732+
LG11	125	0.00	737+
PIO 3995	130	0.30	—
Northern U.S.			
INRA260	135	0.00	739+
EDO	135	0.30	—
A654 × F2	135	0.00	751+
DEKALB × L71	140	0.30	—
F478 × W705A	140	0.00	670+
PIO 3901	144	0.30	—
NE, IA, IL, NC			
PIO 3720	180	0.80	685
A632 × W117	187	0.00	730+
PIO 3382	200	0.70	—
PIO 3780	200	0.76	685
C281	202	0.30	685
Southern NE, Southern IA, Southern IL, Southern IN			
PIO 511A	220	0.30	685
PIO 3183	260	0.50	750
W64A × F546	240	0.30	741+
A632 × VA26	240	0.30	766+
W64A × W117	245	0.00	—
NEB 611	260	0.30	720
B14 × 0H43	265	0.80	665
B8 × 153R2	218	0.30	760
Central MS and KS to NC and Southward			
PIO 3147	255	0.76	685
WF9 × B37	260	0.80	710
PV82S	280	0.50	750
PV76S	260	0.50	750
B56 × C131A	318	0.50	700
B73 × Mo17	220	0.52	880
NC + 59	280	0.30	750
McCurdy 6714	265	0.30	825
Tropical Hybrids			
H610	340	0.52	840
PIO ×304C	390	0.52	940

+ Data[45] assumes maturity occurred at 30% grain moisture.

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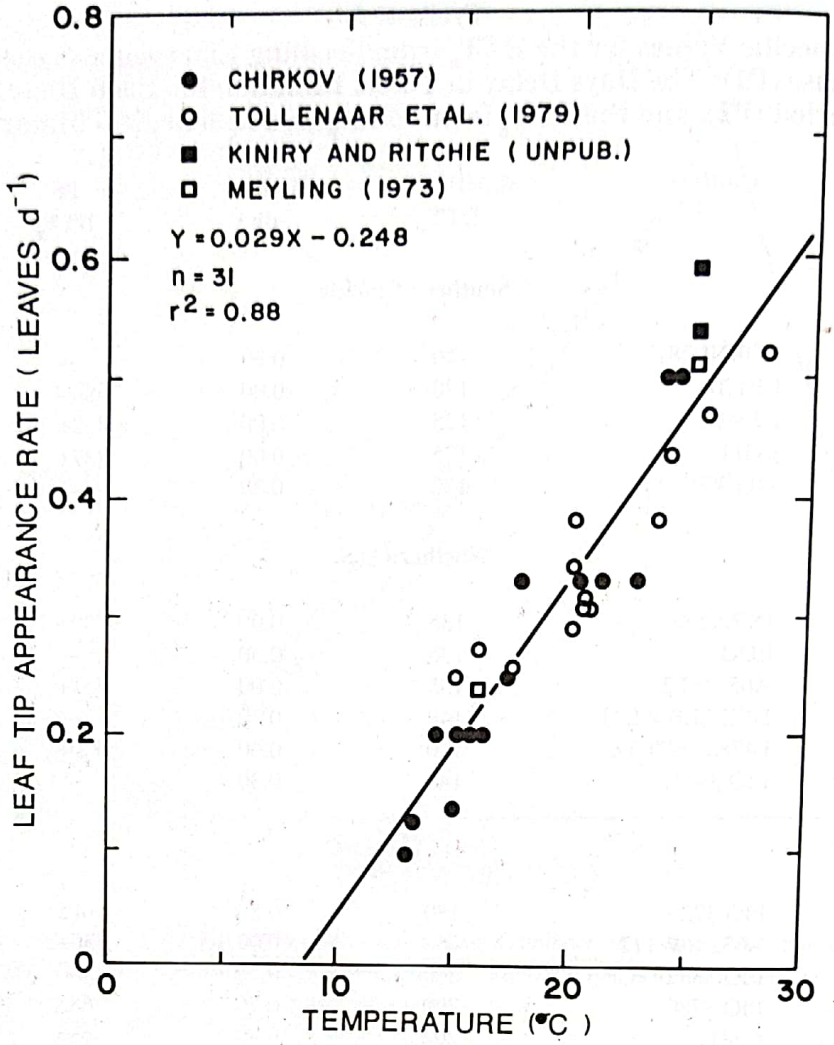

FIGURE 9. Leaf tip appearance rate of maize as a function of temperature with data from four sources.

III. DISCUSSION

A function for possible cooling effects on development rate (Figure 14), derived from unpublished results of Bonhomme and Derieux,[37] was tested on the data of Russell[25] without success. Predictions were less accurate than without the function. Likewise, rate of change of daylength at seedling emergence and error in predictions failed to show any relationship in contrast to the large effect this rate had on phenology of wheat and barley.[38,39] Controlled environment work with maize and wheat[40] also failed to show any relationship between rate of change of daylength and leaf appearance rate.

While results of Warrington and Kanemasu[12] and Bonhomme and Derieux[37] indicate leaf appearance rate per day or per DTT_8 was positively correlated with photoperiod, we did not incorporate this into the model. Gmelig-Meyling[41] failed to find a consistent effect of photoperiod on leaf appearance rate when solar radiation exceeded 200 cal cm^{-2} d^{-1}. Coligado and Brown[4] found a slight decrease in rate of leaf initiation as photoperiod increased from 10 to 20 h. Swan et al.[42] found that inclusion of photoperiod into a leaf emergence model failed to improve predictions.

Likewise, drought effects may show a 1.0 to 1.5 difference in leaf number visible during development, but by silking this difference in development rate will have largely disappeared.[43,44]

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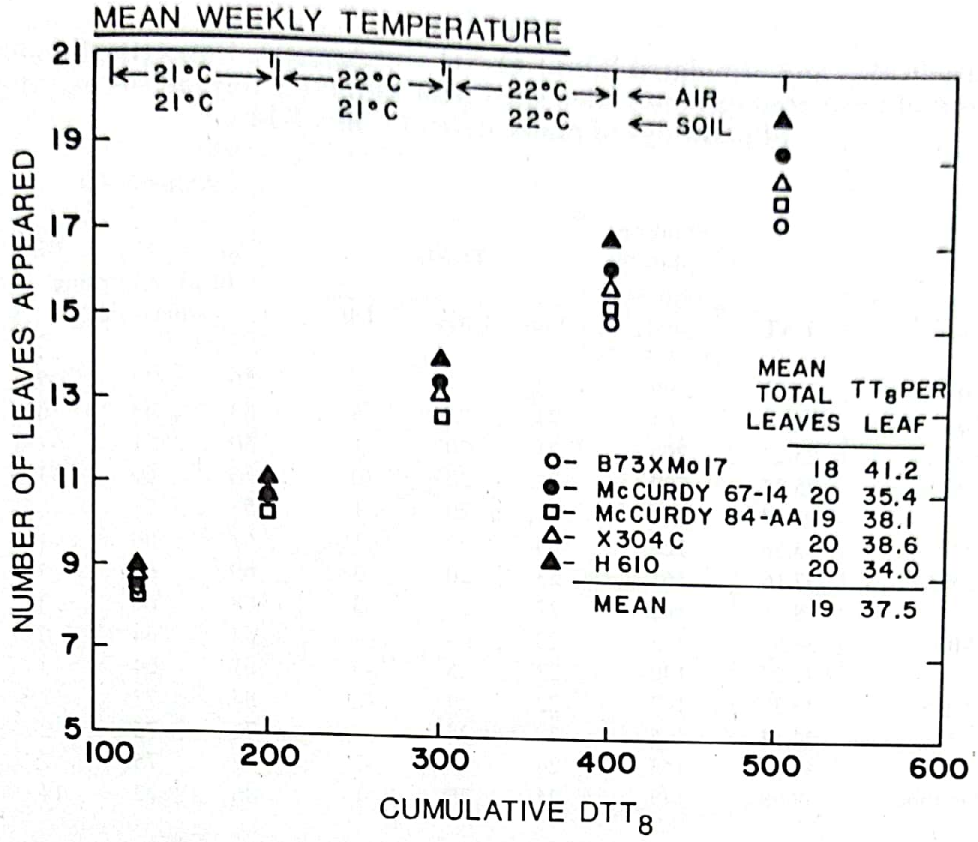

FIGURE 10. Number of leaf tips emerged as a function of cumulative DTT_8 for five maize hybrids grown in the field at Temple, TX.[11]

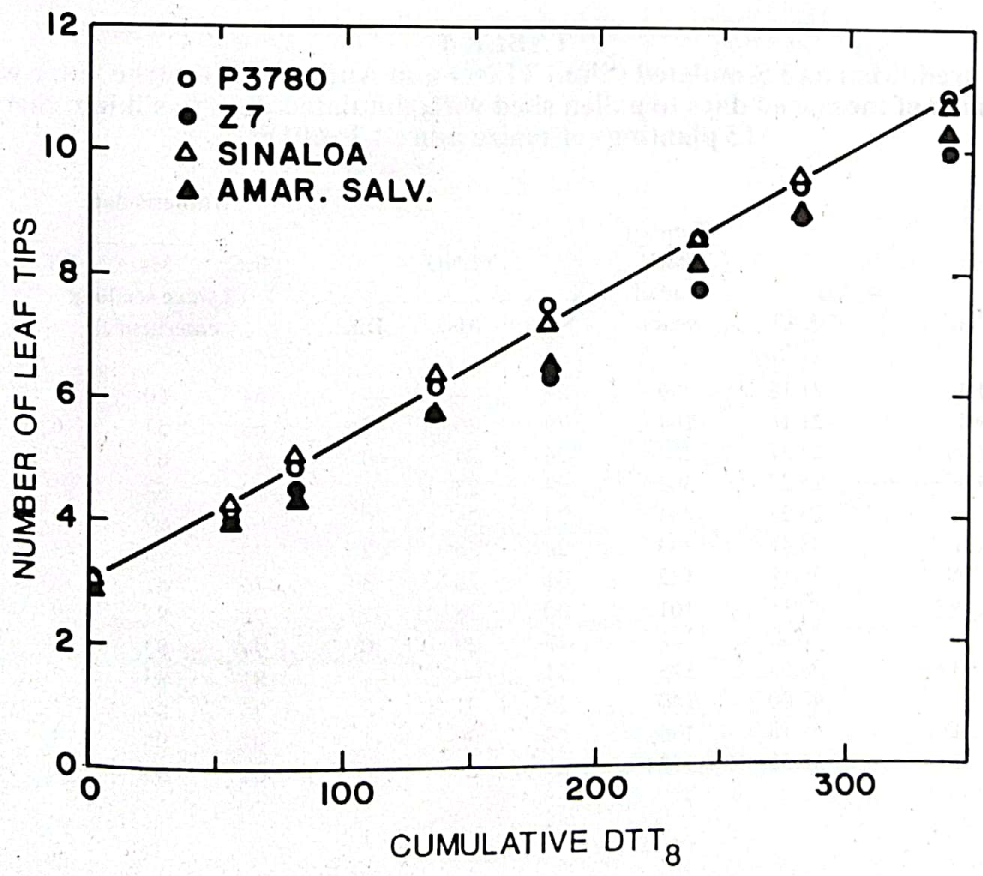

FIGURE 11. Number of leaf tips emerged as a function of cumulative DTT_8 for four maize cultivars grown in the field at Temple, TX.[11]

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TABLE 3
Measured (Ms.) and Simulated (Sim.) TLNO and Anthesis Dates (the latter was a comparison of measured days to pollen shed with simulated days to silking; there were 14 plantings of maize hybrid L36 × B14A)[25]

Location	LAT	Planting date (day of year)	TLNO			Anthesis date (d since seedling emergence)			Temp+ (°C)
			Sim.	Ms.	Dif.	Sim.	Ms.	Dif.	
Honolulu, HI	21.18	99	23	—	—	56	47	9	24.3
Honolulu, HI	21.18	164	24	21	3	53	43	10	25.2
Homestead, FL	25.27	265	21	20	1	50	51	-1	25.3
Homestead, FL	25.27	302	20	20	0	56	69	-13	21.4
Goulds, FL	25.27	284	21	20	1	55	55	0	24.9
Knoxville, TN	35.58	122	23	22	1	61	60	1	24.8
Blacksburg, VA	37.16	161	23	20	3	69	64	5	23.2
Davis, CA	38.33	142	22	25	-3	68	66	2	20.4
Columbia, MO	38.55	123	23	—	—	64	64	0	25.1
Ames, IA	42.00	140	22	25	-3	61	64	-3	16.7
Guelph, Ontario	43.31	147	22	24	-2	84	77	7	18.5
Brookings, SD	44.18	136	22	25	-3	74	76	-2	19.4
Fargo, ND	46.53	143	24	26	-2	77	75	2	21.7
Morden, Manitoba	49.08	143	24	25	-1	86	72	14	16.6
Mean					0			2	
SD					2			6	

+ Mean temperature for the five days centered on the simulated date of tassel initiation.

TABLE 4
Measured (Ms.) and Simulated (Sim.) TLNO and Anthesis Dates (the latter was a comparison of measured days to pollen shed with simulated days to silking; there were 13 plantings of maize inbred Tx601)[25]

Location	LAT	Planting date (day of year)	TLNO			Anthesis date (d since seedling emergence)			Temp+ (°C)
			Sim.	Ms.	Dif.	Sim.	Ms.	Dif.	
Honolulu, HI	21.18	99	27	—	—	64	60	4	25.5
Honolulu, HI	21.18	164	29	26	3	63	57	6	26.2
Homestead, FL	25.27	265	24	24	0	58	65	-7	25.1
Homestead, FL	25.27	302	24	23	1	73	84	-11	23.7
Goulds, FL	25.27	284	25	25	0	67	69	-2	24.3
Miss. St., MS	33.44	99	28	26	2	72	75	-3	22.7
Knoxville, TN	35.58	122	31	28	3	76	81	3	22.2
Blacksburg, VA	37.16	161	30	28	2	90	81	9	24.4
Davis, CA	38.33	142	29	29	0	90	83	7	19.7
Columbia, MO	38.55	123	31	—	—	81	83	-2	23.7
Ames, IA	42.00	140	28	31	-3	75	86	-11	25.3
Brookings, SD	44.18	136	29	30	-1	97	93	4	18.7
Fargo, ND	46.53	143	31	29	2	101	99	22	2.9
Mean					1			-1	
SD					2			7	

+ Mean temperature for the 5 d centered on the simulated date of tassel initiation.

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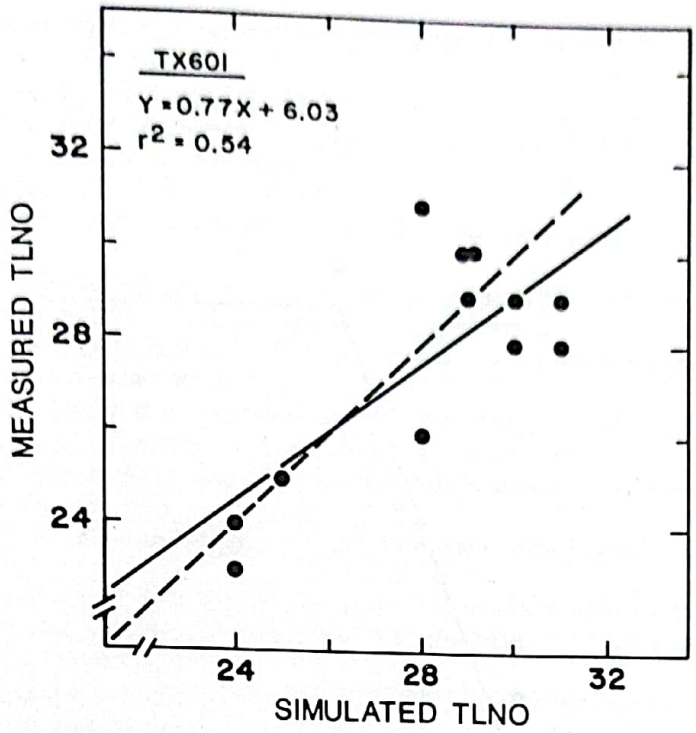

FIGURE 12. A comparison of simulated and measured TLNO for maize inbred Tx601. Data are from Russell.[25]

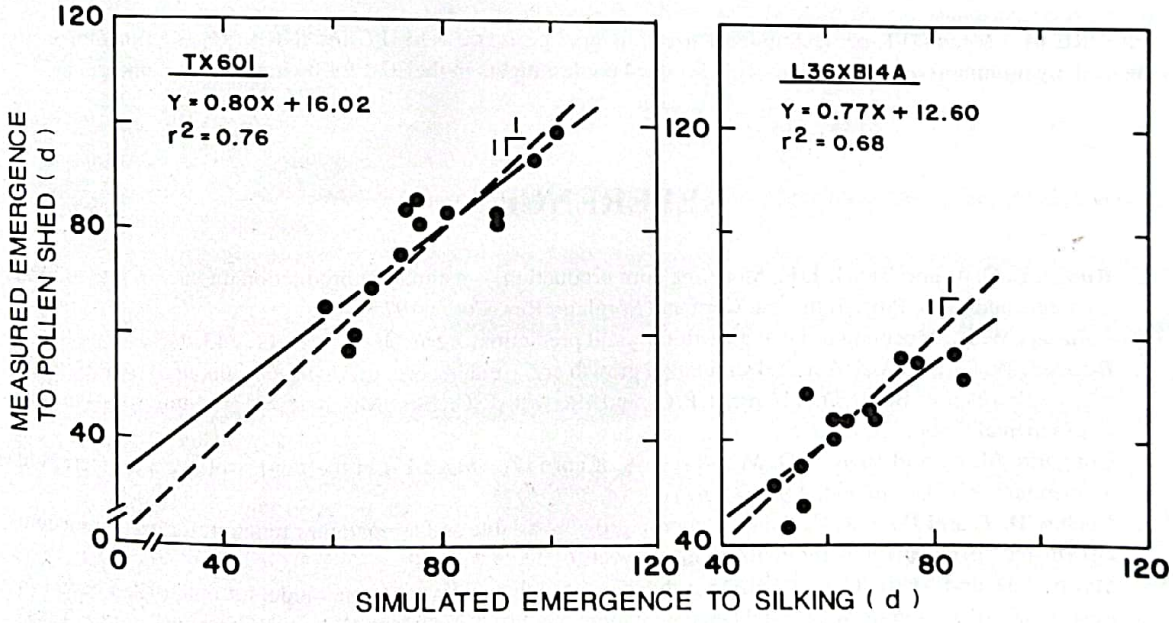

FIGURE 13. Comparisons of simulated days to silking and measured days to pollen shed for maize inbred Tx 601 and maize hybrid L36 × B14A. Data are from Russell.[25]

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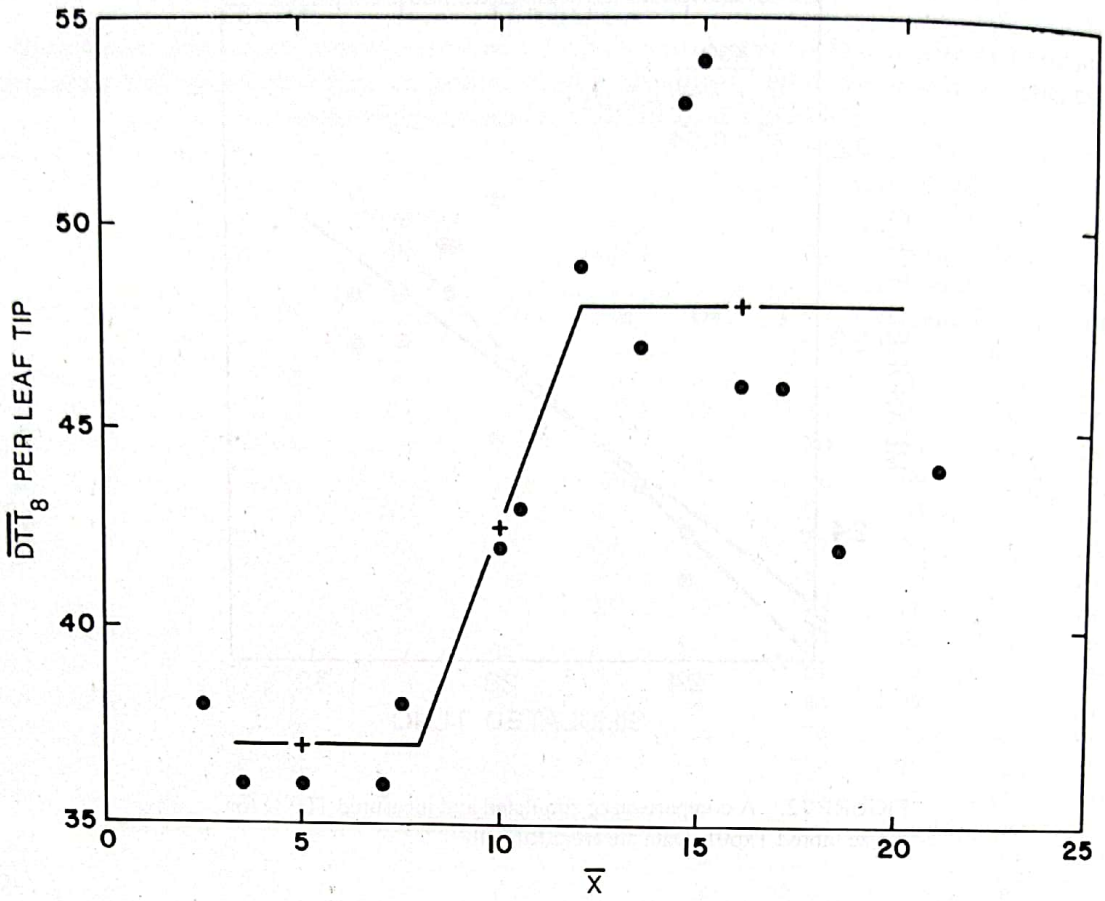

FIGURE 14. Mean DTT_8 per leaf tip for maize cultivars LG11, B73 × Mo17, and INRA 508 as a function of mean daily minimum temperature ($\overline{X}=T_{min}$) for the 4 coolest nights in the 30 d following seedling emergence.

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Chapter 12

THE CERES-WHEAT PHENOLOGY MODEL

Tom Hodges and J. T. Ritchie

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I. INTRODUCTION

The following discussion of the phenology portion of the Crop Estimation through Resource and Environment Synthesis (CERES)-Wheat model is based on version 2.00 of the model computer program provided by J. T. Ritchie. Version 2.00 was released in 1988.

The CERES-Wheat model is a growth simulation model for winter or spring wheat. (CERES is also the name of the Greek goddess of fertility.) The model is written in standard FORTRAN 77, so it can be easily compiled to run on almost any computer — ranging from super computers to microcomputers running MS-DOS or PC-DOS — supporting that language. On a microcomputer, the model requires less than 256K of memory and a hard disk drive or two floppy drives. The model was developed to simulate the growth and development of wheat anywhere it can be grown. It operates on a daily time step and requires daily weather data including solar radiation, rainfall, and maximum and minimum temperatures. In this chapter we discuss the portions of the model dealing with growth stage development and with leaf and tiller initiation, development, and senescence. Dry matter accumulation and partitioning, leaf expansion, photosynthesis, root growth, data requirements, and format of data files will not be discussed. A more complete discussion of all aspects of the model may be found in Otter-Nacke et al.[1]

A. GROWTH STAGES DEFINED

The CERES-Wheat model contains nine growth stages. Stages one through five comprise the periods of above-ground growth. Stage six is the date of maturity. Stage seven is the period from maturity of the last crop to planting of the present crop. Stages eight and nine are germination and emergence. The stages are defined in Table 1.

II. TEMPERATURE CALCULATIONS

A. THERMAL TIME ACCUMULATION

Progress through growth stages is driven by accumulation of daily thermal time (DTT) units. During the emergence to floral initiation (FI) stage, accumulation of DTT units is modified by vernalization and photoperiod factors. Thermal time (TT) is the accumulation of DTT units.

In CERES-Wheat, DTT units are calculated from modified air temperature values (critical temperatures) and base temperature (TBASE) and then accumulated on a daily basis. TBASE is 0°C for stages 1 through 4. It is 1°C for stages 5 through 8, and 2°C for stage 9. Critical temperatures (maximum:TEMPCX, minimum:TEMPCN, and mean:TEMPCR) are used in calculating DTT units. Critical temperatures are equal to their corresponding air temperatures (TEMPCX = TEMPMX, TEMPCN = TEMPMN) except when air temperatures are below freezing. Then they are calculated by Equations 1, 2, and 3:

$$\text{TEMPCN} = 2. + \text{TEMPMN} * \left[0.4 + 0.0018 * (\text{SNOW} - 15) ** 2\right] \quad (1)$$

$$\text{TEMPCX} = 2. + \text{TEMPMX} * \left[0.4 + 0.0018 * (\text{SNOW} - 15) ** 2\right] \quad (2)$$

$$\text{TEMPCR} = \frac{(\text{TEMPCN} + \text{TEMPCX})}{2} \quad (3)$$

where SNOW is snow cover in cm but limited to a maximum value of 15 cm for these calculations. TEMPMX and TEMPMN are maximum and minimum daily air temperatures in °C.

DTT units range from a maximum of 26 when air temperatures are between 26 and 34°C to a minimum of 0 when air temperatures are above 60°C or below 0°C. They are calculated from

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TABLE 1
Growth Stages in the CERES-Wheat Model

1 Emergence to FI
2 FI to begin ear growth
3 Begin ear growth to anthesis
4 Anthesis to begin grain fill
5 Grain fill period
6 Maturity
7 End of the last crop to planting
8 Planting to germination
9 Germination to emergence

Equations 4 through 10. When TEMPCN is above TBASE and TEMPCX is less than 26°C then:

$$DTT = TEMPCR - TBASE \tag{4}$$

which is equivalent to (TEMPMX+TEMPMN)/2 – TBASE when temperatures are greater than TBASE. When air temperatures are outside the range from TBASE to 26°C then the following procedures are used: when TEMPCX is less than TBASE then DTT is set to 0.

If TEMPCN is less than TBASE and TEMPCX is less than 26°C then:

$$DTT = \frac{(TEMPCX - TBASE)}{2} * \frac{(TEMPCX - TBASE)}{(TEMPCX - TEMPCN)} \tag{5}$$

If TEMPCX is greater than 26°C but less than 34°C and TEMPCN is less than 26°C then:

$$DTT = 13.*\left(1+\left[\frac{(TEMPCX - 26)}{(TEMPCX - TEMPCN)}\right]\right)$$

$$+\frac{TEMPCN}{2}*\left[1-\frac{(TEMPCX - 26)}{(TEMPCX - TEMPCN)}\right] \tag{6}$$

If both TEMPCX and TEMPCN are greater than 26°C and less than 34°C then:

$$DTT = 26 \tag{7}$$

If TEMPCX is greater than 34°C and TEMPCN is greater than 26°C then:

$$DTT = \left[\frac{(60 - TEMPCX)*(TEMPCX - 34)}{(TEMPCX - TEMPCN)}\right] + 26*\left[\frac{1-(TEMPCX - 34)}{(TEMPCX - TEMPCN)}\right] \tag{8}$$

If TEMPCX is greater than 34°C and TEMPCN is less than 26°C then:

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$$DTT = \left\{ \frac{(60 - TEMPCX) * (TEMPCX - 34)}{(TEMPCX - TEMPCN)} + 26 * \left[\frac{1 - (TEMPCX - 34)}{(TEMPCX - TEMPCN)} \right] \right\} * \left[\frac{1 - (26 - TEMPCN)}{(TEMPCX - TEMPCN)} \right] + \frac{(TEMPCN + 26)}{2} * \frac{(26 - TEMPCN)}{(TEMPCX - TEMPCN)} \quad (9)$$

DTT ranges from a maximum of 26 when air temperatures are between 26 and 34°C to a minimum of 0 when air temperatures are above 60°C or below 0°C.

B. VERNALIZATION UNITS

Vernalization units (CUMVD) are accumulated daily during stages 9 and 1 when minimum air temperature is less than 15°C and the maximum air temperature is greater than 0°C. During stage one a vernalization factor is calculated daily based on the accumulated vernalization units and the crop genetic coefficient for the vernalization requirement (P1V). Progress through stage 1 will be reduced by the vernalization factor until the plant is fully vernalized. During both stages nine and one, CUMVD is calculated as shown in Equations 11 through 13

$$VD = \text{minimum of} \left[1, \quad 1.4 - 0.778 * TEMPCR, \text{ or } \frac{.5 + 13.44}{(TEMPMX - TEMPMN + 3) * * 2 * TEMPCR} \right] \quad (10)$$

$$VD = \text{maximum of} [0, \quad VD] \quad (11)$$

$$CUMVD = CUMVD + VD \quad (12)$$

Under warm conditions, vernalization can be reversed. If CUMVD is less than 10 and the maximum air temperature is greater than 30°C then:

$$CUMVD = CUMVD - .5 * (TEMPMX - 30) \quad (13)$$

CUMVD is not allowed to be less than 0. Vernalization is complete when CUMVD exceeds 50. Thereafter, vernalization is not calculated.

C. COLD HARDINESS INDEX

During stage 1, the cold hardiness index (HI) is calculated from maximum (TEMPMX) and minimum air temperatures (TEMPMN), TBASE (0°C), and TEMPCR. HI is used to reduce damage in calculating winter kill of leaves, tillers, and plants. Calculation of HI is started on the first day during stage 1 when TEMPMN is less than or equal to TBASE less 3°C. Thereafter, HI is recalculated daily for the duration of stage 1 as long HI remains above 0 or if TEMPMN drops below –3°C. If HI is less than 1 and TEMPCR is between –1 and 8°C then HT1 will be added to HI:

$$HI1 = \frac{.1 - (TEMPCR - 3.5) * * 2}{506} \quad (14)$$

If HI plus HT1 is less than 1 and TEMPCR is between –1 and 8°C or if HI is greater than 1 and TEMPCR is less than 0°C then:

$$HT2 = 0.083 \quad (15)$$

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If HI + HT1 + HT2 is greater than 2 then:

$$HT2 = 2 - HI - HT1 \tag{16}$$

If TEMPMX is greater than 10°C and either HI is greater than 1 or TEMPCR is greater than 8°C then:

$$HI = HI + .2 - .02 * TEMPMX \tag{17}$$

If HI plus HT1 plus HT2 is greater than 1 then execute Equation 17 again. Finally:

$$HI = HI + HT1 + HT2 \tag{18}$$

If HI is less than 0 then HI is set to 0. The result of the above is that HI varies from 0 to 2.

D. PHOTOPERIOD

Daylength or civil twilight is calculated from day of the year (DOY) and latitude (LAT) during stage 1 once 30% of the vernalization requirement has been met. The daylength equations are as follows:

$$S1 = SIN(LAT * 0.01745) \tag{19}$$

$$C1 = COS(LAT * 0.01745) \tag{20}$$

$$DEC = 0.4093 * SIN[0.0172 * (DOY - 82.2)] \tag{21}$$

$$DLV = \left[\frac{(-S1 * SIN(DEC) - 0.1047)}{(C1 * COS[DEC])}\right] \tag{22}$$

$$IF\ (DLV.LT.-0.87) \qquad DLV = -0.87 \tag{23}$$

$$HRLT = 7.639 * ACOS(DLV) \tag{24}$$

where S1, C1, DEC, and DLV are variables used in the calculations, and HRLT is duration of civil twilight.

E. PHYLLOCHRON INTERVAL

The phyllochron interval (PHINT) is the number of TT units needed for the appearance of each phyllochron unit on the plant (i.e., a leaf or a tiller). PHINT is used to account for poorly understood variability in the appearance rate of leaves and tillers with respect to latitude and date of planting. It varies with variety, LAT, and time of planting, from about 60 to 120. A mean value is about 95. If accuracy is necessary, the TT between leaf tip appearances should be measured for the sowing time of interest to the model user.

III. GROWTH STAGE CALCULATIONS

A. END OF THE PREVIOUS CROP TO PLANTING (ISTAGE=7)

This stage starts with the beginning of the simulation (an input to the model) or with stage six of the previous crop and ends with the planting date.

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B. PLANTING TO GERMINATION (ISTAGE=8)

If soil moisture in the soil layer where seed was planted is above the lower limit volumetric water content (approximate wilting point; see Jones and Kiniry[2] for a precise definition of lower limit volumetric water content) germination occurs the day after planting. If the planting layer is dry, then the following equation is used to determine whether sufficient moisture is present for germination to occur:

$$SWSD = (SW(L0) - LL(L0))*.65 + (SW(L0+1) - LL(L0+1)*.35) \quad (25)$$

where L0 is the planting layer of the soil, L0+1 is the next lower soil layer, SW is the volumetric soil water content of a layer and LL is the lower limit volumetric water content of a layer. If SWSD is greater than 0.02 then germination occurs. If neither of the above conditions are met by 90 d after planting, crop failure is declared by the model and the run is ended.

C. GERMINATION TO EMERGENCE (ISTAGE=9)

This period is calculated in accumulated DTT units, based on the depth of planting (SDEPTH in centimeters) as follows:

$$P9 = 40 + 10.2 * SDEPTH \quad (26)$$

where P9 is the thermal time required for emergence.

D. EMERGENCE TO FLORAL INITIATION (ISTAGE=1)

Leaf and tiller initiation occur until FI, which in CERES-Wheat is controlled by vernalization, TT, and photoperiod factors with crop genetic coefficients controlling the sensitivity of the model to vernalization and photoperiod. P1V controls sensitivity to vernalization, P1D controls sensitivity to photoperiod, and PHINT (the size of the phyllochron interval) determines the amount of TT (modified by the vernalization and photoperiod factors) needed for the stage. The vernalization factor (VF) is calculated from CUMVD as:

$$VF = 1 - P1V * (50 - CUMVD) \quad (27)$$

If VF is greater than 1 then VF is set to 1. The photoperiod factor (DF) is calculated from daylength (HRLT) when VF is greater than 0.3 as:

$$DF = 1 - P1D * (20 - HRLT) \quad (28)$$

Thermal time (TT) is accumulated from DTT, VF, and DF as:

$$TT = TT + DTT * \text{ minimum of } [VF, \quad DF] \quad (29)$$

The thermal time needed for the stage is 400*PHINT/95.

E. FLORAL INITIATION TO BEGIN EAR GROWTH (ISTAGE=2)

Stage two ends when 3*PHINT DTT units have accumulated after the end of stage one.

F. BEGIN EAR GROWTH TO ANTHESIS (ISTAGE=3)

Stage 3 ends when 5*PHINT DTT units have accumulated after the end of stage 1.

G. ANTHESIS TO BEGIN GRAIN FILL (ISTAGE=4)

Stage 4 ends when 200 DTT units have accumulated after the end of stage 3.

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H. GRAIN FILL PERIOD (ISTAGE=5)

Stage five ends when P5 DTT units have accumulated after the end of stage four. P5 is a crop genetic coefficient which ranges from 450 to 530 in data provided with the model.

I. MATURITY (ISTAGE=6)

This stage lasts for 1 day after the end of stage 5.

IV. TILLER INITIATION AND SENESCENCE

Tiller initiation occurs during stages one, two, and three. During stage one, tiller number (TILN) increases with DTT. The rate of increase is enhanced by accumulated phyllochron units (CUMPH, a function of accumulated DTT) and is slowed by water and nitrogen stress. If the water or nitrogen stress factors are sufficiently low, or if tiller density is greater than 3000/m^2, then tiller numbers will decrease.

Cold damage may also reduce tiller number during stage one. Cold damage to tillers occurs whenever the TEMPCR is less than the killing temperature (TEMKIL). The killing temperature is calculated as:

$$\text{TEMKIL} = \text{TBASE} - 6. \quad - 6.*\text{HI} \tag{30}$$

Tiller death is calculated as:

$$\text{TILN} = \text{TILN} * (0.9 - 0.02 * (\text{TEMPCR} - \text{TEMKIL}) * *2) \tag{31}$$

If this results in less than 1 tiller/plant, then tiller number is set to 1 and the number of plants is reduced:

$$\text{PLANTS} = \text{PLANTS} * (0.95 - 0.02 * (\text{TEMPCR} - \text{TEMKIL}) * *2) \tag{32}$$

If PLANTS (number of plants/m^2) is less than 5 then a message is displayed that 95% of the crop has been killed by cold and the run is terminated.

At the end of stage one, tiller number is reduced to 1000/m^2 if it is greater than that.

During stages two and three, TILN will increase or decrease depending on a complex function balancing stem weight against maturity, water and nitrogen stresses, and current tiller number. High stem weight will cause TILN to increase. High TILN and increased maturity will cause TILN to decrease. The crop genetic coefficient G3 is inversely related to change in tiller number during stages two and three.

V. LEAVES

A. INITIATION

During stages one and two, leaf number on the mainstem (LN) increases with increases in accumulated DTT divided by PHINT (the number of thermal time units for development of one phyllochron):

$$\text{CUMPH} = \text{CUMPH} + \frac{\text{DTT}}{\text{PHINT}} \tag{33}$$

$$\text{LN} = \text{CUMPH} + 2 \tag{34}$$

B. GROWTH

During stage one, potential leaf area expansion is positively related to increasing air temperature up to 17°C, CUMPH and TILN up to 900 tillers/m^2. It is reduced by air temperatures above

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17°C, water stress, and nitrogen stress. During stage two, leaf area expansion is only limited by the amount of carbohydrate remaining after root and stem growth demands have been satisfied.

C. SENESCENCE

Leaf area may die due to either age or to stresses such as freezing, drought, or nitrogen shortage.

D. AGING

During stages one and two, if LAI is greater than 6.0 or if the senesced leaf area is less than 40% of the total leaf area, then the leaf area added between the appearance of the 6th and 5th oldest leaves times the fraction of a phyllochron unit accumulated during the current day is lost. If this would reduce the leaf area per tiller to less than 0.035 cm^2 then the loss is limited so that leaf area per tiller remains at 0.035 cm^2. The effect of this is to limit the number of leaves on any plant to six full leaves per tiller. During stage three, 0.03% times DTT of the green leaf area is lost each day due to aging. Since DTT may vary from 0 to 26, up to 0.78% of the green leaf area may be lost in a day. During stage four, 0.06% times DTT of the green leaf area is lost each day due to aging.

E. COLD DAMAGE

A leaf cold damage factor (CK) is calculated during stage one from the cold HI, TEMPMX and TEMPMN and the depth of snow cover as:

$$CK = (0.02 * HI - 0.1) * (TEMPMN * 0.85 + TEMPMX * 0.15 + 10. + 0.25 * SNOW) \quad (35)$$

If CK is less than 0 then CK is set to 0. If CK is greater than 0.96, CK is set to 0.96. Leaf death is equal to green leaf area times CK. Cold damage is not allowed to kill all the leaves, at least 0.5 cm^2/tiller are not killed.

F. WATER AND NITROGEN STRESS

If the water stress variable SWDF1, which may vary from 1.0 to 0.0, is less than 0.8, then water and nitrogen stress effects on leaf senescence are calculated. Leaf area loss due to aging is multiplied by the lesser of W1 and SN1:

$$W1 = 2.0 - \frac{SWDF1}{0.8} \quad (36)$$

$$SN1 = 2.0 - \frac{NDEF4}{0.8} \quad (37)$$

where NDEF4 is a nitrogen stress variable that may vary from 1.5 to 0.0004. If SWDF1 is less than 0.8, then a high level of nitrogen may reduce leaf loss due to aging to 1/8 of its normal level.

VI. MODEL VALIDATION

The model was tested against both independent and dependent data sets by Otter-Nacke et

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al.[1] They found mean errors of 5 d for anthesis and heading dates for the independent data and of 7 d for the dependent data. Root mean square errors ranged from 6 to 12 d. French and Hodges[3] used the model to predict jointing, heading, soft dough, and maturity dates for crop reporting districts in Kansas for 15 years. The root mean square errors were 4.5, 3.3, 2.9, and 3.4 days for jointing, heading, soft dough, and maturity, respectively.

VII. SUMMARY

Use of the model has been reported over a wide range of environments[1,3] with acceptable results. The model deals with most major physiological growth processes. It is one of a family of models using common data file formats, common weather and soils data, and identical or nearly identical soil water and soil nitrogen submodels. Other models in the family include those for maize, soybean, peanut, drybean, rice, sorghum, and potato.

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Chapter 13

PHASIC DEVELOPMENT IN CERES-SORGHUM MODEL

G. Alagarswamy and J. T. Ritchie

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I. INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is one of the principal sources of calories in the semi-arid tropics (SAT), while in the nonSAT sorghum growing countries it is used mostly as an animal feed. Sorghum is grown in about 49 million hectares producing 72 million metric tons of grain.[1] Though sorghum was domesticated in Ethiopia, it is now grown in latitudes ranging from 35 degrees south to 45 degrees north of the equator. Genetic variations in the phenology offer a choice of cultivars to fit such diverse growing conditions.

The success of local landraces of several crops, especially sorghum and pearl millet in West Africa, is due to the adaptability of the plants. In Nigerian sorghums, this adaptability ensures that the date of heading occurs close to the end of the local rains, so that grain matures as the weather becomes dry.[2] This feature is very important, as growing season length is estimated to decrease at the rate of 19 d for each degree change of latitude northward in West Africa.[3] The length of time during which the plant grows is one of several factors influencing crop productivity. In general, the yield potential of a crop increases with the increase in the length of growth duration. Similarly, the biomass produced at flowering stage in sorghum is also related to days to flowering.[4] When length of growing season is limited, as in West Africa, fitting a crop to the season length is still the key to successful farming. Thus, grain yield improvements in these regions requires a clear understanding of developmental morphology of the sorghum plant.

Mechanistic crop simulation models have been used as an analytical tool to understand complex agricultural systems. In addition to this general use, highly mechanistic and comprehensive models have been more imaginatively used to evaluate potential alternate management practices that influence yield and yield-forming processes. Several simulation models for a number of crops are available.[5] Most of them are site specific. For any model to be truly generic, it should be able to accurately predict performance of a cultivar sown at any time, on any soil, and in any climate. This goal is certainly difficult to achieve. However, if a comprehensive, mechanistic model could simulate phasic development with reasonable accuracy on any site, especially as it is affected by genetics and climate, then part of the requirement for a generic goal can be fulfilled. A unique feature of the Crop Estimation through Resource and Environment Synthesis (CERES) models lies in their considerable ability to do this. Describing the steps involved in developing the phenology subroutine in the CERES-Sorghum model is the objective of this paper.

II. THERMAL TIME ESTIMATION

Temperature influences the rate of several developmental processes. Daily progression of plant development in several crops has been precisely described by the growing degree day (GDD) approach,[6,7] which relates developmental rates to air temperature. Below a certain minimum temperature no plant development takes place, and above an optimum temperature the development rate decreases drastically. Between these two defined temperatures, plant development rate increases linearly with the increase in temperature.[7-9] The number of leaf tips that appear on a mainstem can indicate the state of plant development. The leaf tip appearance rate can also provide a measure of the rate of development. In this work we use such an approach. Leaf tip appearance was measured for several sorghum genotypes at temperatures ranging from 11 to 40°C in growth chambers. Leaf appearance rate was 0 at 8°C. This was designated as base temperature (TBASE). Beyond 34°C leaf tip appearance rates declined drastically. Between this lower and upper temperature limit leaf tips appear as a linear function of temperature.[10] These results were used to calculate daily thermal time (DTT) accumulation.

When the daily minimum temperature (TEMPMN) is above TBASE and daily maximum temperature (TEMPMX) is below 34°C, DTT in the model is calculated as:

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TABLE 1
Growth Stages of Sorghum as Defined in CERES-Sorghum Model

Growth stage	Description of the stage	Plant parts that grow
7	Presowing	
8	Sowing to germination	
9	Germination to seedling emergence	Roots, coleoptile
1	Seedling emergence to end of juvenile stage	Roots, leaves
2	End of juvenile stage to PI	Roots, leaves
3	PI to end of leaf growth	Roots, leaves, stem
4	End of leaf growth to beginning of effective grain filling	Roots, stem, panicle
5	Effective grain filling to physiological maturity	Roots, stem, grain
6	Physiological maturity to harvest	

$$DTT = \frac{(TEMPMX + TEMPMN)}{2.0} - TBASE$$

When TEMPMN is less than TBASE and TEMPMX is greater than 34°C, a different method is followed to calculate DTT. In such circumstances, interpolations between the maximum and minimum temperatures (TTMP) is calculated using an approximated average temperature of each 3-h period through the day. This approximation is obtained through use of a temperature correction factor (TMFAC).

$$TMFAC(I) = 0.931 + 0.114 * I - 0.0703 * I**2 + 0.0053 * I**3$$

$$TTMP = TEMPMN + TMFAC(I) * (TEMPMX - TEMPMN)$$

where I = 1.8. For each value of TTMP, a 3-h value of DTT is calculated. If TTMP is between TBASE and 34°C then:

$$DTT = DTT + \frac{(TTMP - TBASE)}{8.0}$$

When leaf appearance rate was extrapolated beyond 40°C, rates reached 0 at 52°C.[10] Therefore, when TTMP value is between 34 and 52°C then:

$$DTT = DTT + \frac{(34.0 - TBASE) * \left(1.0 - \frac{(TTMP - 34.0)}{18.0}\right)}{8.0}$$

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These 3-h estimates of DTT are then used to obtain a value of DTT for that day. Adjusting the DTT calculation in this way takes into account the effects of unfavorable temperatures on the duration of any developmental stage.

DTT values are summed up to obtain an accumulated thermal time. There are two variables, SUMDTT and CUMDTT, that give accumulated DTT, but the values of SUMDTT are set to zero at seedling emergence, panicle initiation (PI), end of leaf growth, end of panicle growth, and physiological maturity. The SUMDTT values are used to determine the duration of various phenological stages and to drive the model through time. The CUMDTT values are used to indicate the accumulated DTT from seedling emergence at any given time.

III. ORGANIZATION OF PHASIC DEVELOPMENTAL STAGES

Phasic development in the CERES-Sorghum model describes the duration of several growth stages. Growth stages are organized to strictly follow the dynamic nature in which the plant allocates assimilates to various organs. Assimilates are partitioned entirely between leaves and roots prior to PI. After PI, various organs, such as stem, leaf, root, and panicle grow simultaneously and begin to compete for the assimilates. Immediately prior to anthesis the rapidly growing panicle becomes the most active sink for assimilates. After anthesis, developing grains are the major sink for assimilates. The various growth stages are organized, as in other CERES models, around times when partitioning of assimilates changes among plant organs.

Growth stages in the model are numerically coded (Table 1). This coding system assists in routing the control through the major growth and phenology subroutines of the model. Various plant organs actively grow between stages one and five. While stage six is not presently used in the model, it can be used to model postmaturity changes in seeds. Stages seven through nine are used to describe other events occurring between sowing and seedling emergence.

IV. DESCRIPTION AND MODELING GROWTH STAGES

The CERES-Sorghum model has a MAIN program which, at the beginning of model execution, opens several input and output files. Several other subroutines are then called to read input data and to initialize a number of variables. The MAIN program then enters into a daily loop and reads day of year (JDATE), solar radiation (SOLRAD), TEMPMN, TEMPMX and precipitation (RAIN) from the weather file, at which time the subroutine WATBAL is called to simulate water balance. After simulating water balance, subroutine PHENOL is called by the MAIN program to simulate rate of development. Whenever a growth stage (ISTAGE) is completed, subroutine PHASEI is called to initialize variables that will be used in the following growth stage. Each time PHASEI is called ISTAGE is updated.

A. STAGE 7: PRESOWING

On the sowing date the subroutine PHENOL is called by the MAIN program. To calculate the days since sowing, a day-counter (NDAS) is created and its initial value is set to zero. The soil layer in which the seed is sown (L_0) is determined using sowing depth (SDEPTH) and soil layer thickness (DLAYR) This stage in the model could also be used to simulate soil-water balance when the initial soil-water condition at the time of sowing is unknown. If the water balance is run, the soil water content can be assumed to be either uniformly dry (when the previous crop was harvested) or uniformly wet (when rainfall occurs).

B. STAGE 8: SOWING TO GERMINATION

Besides seed quality and dormancy, the two most important factors affecting seed germination are soil moisture at seeding depth and soil temperature. The minimum temperature for germination is set to 10°C. If temperature is favorable, then the soil moisture content in the

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seeding zone is determined. If the soil moisture in that layer ($SW[L_0]$) is greater than the lower limit (LL) of extractable water, the seed will germinate. If the soil moisture in that layer is less than the LL, a weighted average water content of the first and second soil layer (SWSD) is calculated to determine whether or not the seed can germinate.

$$SWSD = \left(SW(L_0) - LL(L_0)\right) * 0.65 + \left(SW(L_0 + 1) - LL(L_0 + 1)\right) * 0.3$$

If the value of SWSD is greater than or equal to 0.02, seed germinates.

Sowing sorghum under dry conditions is a common practice, and seed must await rain for germination. If the soil is too dry for the seed to germinate, day counter NDAS is used to calculate such dry days since sowing. If NDAS values reach 40 and if the seed did not germinate for lack of soil moisture, the crop is assumed to have failed. A crop failure message is then written. When soil moisture is sufficient, seed germinates and the initial rooting depth (RTDEP) is set to sowing depth (SDEPTH).

C. STAGE 9: GERMINATION TO SEEDLING EMERGENCE

Seedling emergence is influenced by temperature and the depth of sowing. Temperature affects thermal time accumulation, while depth of sowing influences the length of time necessary for the coleoptile to reach the soil surface. Seedlings emerge when the thermal time reaches the value of the coefficient P9 (TBASE = 10°C). The duration of this stage is determined by:

$$P9 = 20.0 + 6.0 * SDEPTH$$

Prior to seedling emergence RTDEP increases linearly with DTT.

$$RTDEP = RTDEP + 0.15 * DTT$$

D. STAGE 1: SEEDLING EMERGENCE TO END JUVENILE STAGE

During this stage plants grow vegetatively and produce leaf primordia. The development rate is controlled by temperature. Since plants are not sensitive to photoperiod in this stage, knowing when this stage is complete is important in order to implement photoperiod sensitivity relationships. The juvenile stage ends when SUMDTT equals or exceeds the value of P1. The coefficient P1 is estimated as described by Kiniry et al.[11] Maturity genes affect the length of juvenile period. Late maturing genotypes have a longer juvenile phase compared to early maturing genotypes. Such genetic differences in the duration of this period are accounted for in the model by a genotype specific coefficient P1. In this way, the model acknowledges that plants must reach a certain size or produce a certain number of leaves before they become sensitive to photoperiod.

E. STAGE 2: END OF JUVENILE STAGE TO END OF PANICLE INITIATION (PI)

During this stage plants are still producing leaf primordia. Only at the end of this stage does the pattern of cellular activity in the apical meristem change from leaf primordia production to floral primordia production. The development rate is strictly controlled by favorable photoperiod. Since sorghum plants exhibit a quantitative, short photoperiod, response, daylengths longer than 12 h delay development. Daylength and sensitivity of genotypes to photoperiod determine the duration of this stage.

At first, daylength (HRLT) is calculated as a function of solar declination (DEC in radians), sine and cosine of latitude (LAT) and angle of sun at civil twilight. DEC is a sine function of JDATE.

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$$DEC = 0.4093 * SIN[0.0172 * (JDATE - 82.2)]$$

Daylength variation (DLV) is derived from sine and cosine of LAT and DEC. It is adjusted for sun angle at civil twilight.

$$DLV = \frac{(-SIN(LAT) * SIN(DEC) - 0.1047)}{[COS(LAT) * COS(DEC)]}$$

As boundary conditions minimum value of DLV is set to –0.87. HRLT is then an arc cosine function of DLV.

$$HRLT = 7.639 * ACOS(DLV)$$

Second, the sensitivity of genotypes to photoperiod is derived as noted in several crops.[12-14] Thermal time from seedling emergence to PI could be expressed in two photoperiod response ranges, namely an insensitive and a sensitive range.

In the insensitive range, changes in daylength have no effect on thermal time for PI. There is a threshold photoperiod (P2O) above which thermal time for PI increases linearly with increasing photoperiod. The slope (TT per hour increase in daylength) is termed as Photoperiod Sensitivity Coefficient (P2R). Growth chamber studies at 25°C constant temperature indicated that the duration of floral induction in sorghum lasted for 102 degree days when HRLT is below P2O.

In the model, rate of floral induction (RATEIN) is calculated from HRLT and genotype specific coefficients P2O and P2R. If HRLT is less than or equal to P2O, RATEIN is a constant (1/102). If HRLT is greater than P2O, then RATEIN is reduced to an extent depending on P2R and HRLT beyond P2O. The product of RATEIN and DTT is summed daily with a temporary variable SIND.

$$RATEIN = \frac{1.0}{[102.0 + P2R * (HRLT - P20)]}$$

$$SIND = SIND + RATEIN * DTT$$

When the value of SIND reaches unity, stage two is completed. The duration of this stage is therefore dependent upon daylength above P2O and P2R. Another unique feature of the CERES models is the emphasis on the duration of this stage as influenced by genetic differences among genotypes. The genotype response to changes in photoperiod ranges from insensitive to highly sensitive. Genetic coefficients for P1, P2O and P2R for widely different sorghum genotypes are given in Table 2.

F. STAGE 3: PI TO END OF LEAF GROWTH

Duration of this stage is from PI until flag leaf expansion and is temperature dependent. All leaf tips appear and the final leaf completes its expansion growth. Stem growth starts in the earlier part of this stage and eventually becomes a competing sink for assimilates. This stage is completed when SUMDTT equals or exceeds the constant P3. The magnitude of P3 was determined from the phenology data reported by Scheaffer[15] for four sorghum hybrids at several dates of planting in Kansas. In this study, thermal time for flowering (DTT AN) was directly related to thermal time for PI (DTT PI) as described by Equation 1:

$$DTT\ AN = 1.199 * DTT\ PI + 450.0 \quad (1)$$

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TABLE 2
Genetic Constants for Duration of Juvenile Stage (P1, Degree Days), Threshold Photoperiod (P2O, in h) and Photoperiod Sensitivity Coeff. (P2R, degree days per h) for Diverse Sorghum Genotypes

	Genotypes	P1	P2O	P2
1	Rio	430	11.6	24
2	9188	393	13.0	23
3	Brandes	374	11.0	116
4	MN 1500	495	11.8	139
5	Hegari	273	11.5	136
6	100 M	291	11.0	127
7	80 M	337	12.6	262
8	60 M	337	12.8	290
9	SM 100	365	13.0	45
10	SM 80	356	12.0	74
11	SM 60	365	12.2	74
12	Redlon	393	12.5	30
13	Caprock	393	12.8	84
14	ATx 378 / RTx 7000	384	11.3	24
15	ATx 623	380	13.0	35
16	RTx 430	400	13.0	123
17	ATx 623 / RTx 430	390	13.0	35
18	BTx 3197	411	13.0	108
19	RTx 7078	421	14.4	221
20	RS 610	275	15.5	30
21	Wheatland	365	12.5	30
22	ATx 399 / RTx 430	393	12.8	40
23	ATx 378 / RTx 430	411	12.5	20
24	ATx 623 / RTx 7000	374	13.0	14
25	38 M	291	13.0	12

Since DTT AN is composed of DTT PI and thermal time to reach flowering after PI (DTTPD). Equation 1 can also be written as:

$$\text{DTT PI} + \text{DTT PD} = 1.199 * \text{DTT PI} + 450.0 \quad (2)$$

DTT PD could be estimated from Equation 2.

$$\text{DTT PD} = 0.199 * \text{DTT PI} + 450.0 \quad (3)$$

From the studies conducted at Colorado, in which several sorghum genotypes were used, thermal time from flag leaf expansion until flowering in several sorghum genotypes was estimated to be 150 degree days.[16] After accounting for this from the thermal time value 450.0 in Equation 3, thermal time for completing the leaf development (P3) could be estimated with the following equation:

$$P3 = 0.199 * \text{DTT PI} + 300.0$$

G. STAGE 4: END OF LEAF GROWTH TO BEGINNING OF GRAIN FILLING

During this stage the panicle develops rapidly and the peduncle grows quickly, extending the panicle through the flag leaf sheath. Duration of this stage is assumed to be constant for all genotypes at 270 degree days with flowering assumed to occur after completing 150 degree

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TABLE 3
Summary and Difference Measures for Phenology Data to Evaluate the Association between Observed and Simulated Values in Two Data Sets

Location & stage	Summary and different measures@								
	n	o	p	So	Sp	a	b	RMSE	r^2
Hyderabad									
PI	12	208	210	11.9	12.2	0.65	1.01	2.51	0.97
Flowering	12	244	241	13.2	12.6	20.0	0.91	4.29	0.90
Maturity	12	276	276	14.5	13.1	44.0	0.84	5.50	0.85
Texas									
PI	44	182	180	45.5	46.2	3.1	1.00	5.91	0.98
Flowering	44	207	211	47.5	48.3	1.6	0.97	6.89	0.98
Maturity	40	232	221	41.5	43.1	8.9	0.99	12.85	0.91

@ n = Number of observations.
o = Mean of observed value.
p = Mean of simulated value.
S_o = Standard deviation of observations.
S_p = Standard deviation simulated values.
a = Intercept of regression of simulated on observed.
b = Slope term from regression of simulated on observed.
RMSE = Residual mean square error.
r^2 = Coefficient of determination.

days.[16] The panicle accumulates most of the dry matter but the stem becomes a temporary sink storing the excess assimilates, which later could be translocated to the rapidly growing grains.

H. STAGE 5: EFFECTIVE GRAIN FILLING TO PHYSIOLOGICAL MATURITY

Most of the assimilates are partitioned to the panicle during this stage, when grain is rapidly growing. At the beginning of this stage the grain has attained the approximate volume it will have at maturity. Because grain grows rapidly, the rate of mass accumulation in seeds is approximately linear. Grain growth represents storage of assimilates from current photosynthesis and relocation from stems. Physiological maturity coincides with maximum grain dry weight accumulation. Thermal time needed for the grain filling stage is input as genetic coefficient P5. Even though considerable variation for the duration of grain growth has been shown among genotypes,[17,18] most of the commonly grown genotypes require about 550 degree days to reach physiological maturity. When cumulative thermal time values reach or exceed P5, physiological maturity occurs. If thermal time is less than 2 degree days for 3 consecutive days, then the crop is assumed to mature early. This allows physiological maturity to occur early at sustained low temperatures. The crop is also assumed to mature if the minimum temperature falls below 0°C.

I. STAGE 6: PHYSIOLOGICAL MATURITY TO HARVEST

This stage is reserved for users who may want to model possible yield reductions arising due to inability to harvest the crop in time.

V. MODEL VALIDATION

Before the model can be widely used, it needs to be adequately tested with independent data sets. The accuracy of phenology prediction is very important, since assimilate allocation to different plant parts is entirely dependent upon the type of plant organs that grow in any particular growth stage. The phenology predictions were tested using two independent data sets from vastly different sorghum growing regions.

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The first data set was extracted from an unpublished dissertation. In this study, a widely adapted temperate hybrid, RS 610, a tropically adapted hybrid, AT× 623 × RT× 430, and tropically adapted lines AT×623 and RT×430 were grown in a serial date of planting experiment at three locations in Texas. The genotype specific coefficients for these genotypes are given in Table 2. The data clearly demonstrate that these genotypes are different in their photoperiod sensitivity coefficients. The second data set was taken from a multi-location modeling experiment.[19] In this study a single sorghum hybrid CSH 1 was grown at several locations (LAT ranging from 11 to 31N). Numerous statistical measures as suggested by Otter-Nacke et al.[20] were used to evaluate the association between observed and modeled values for phenology stages. Test criteria using summary and difference measures for both locations are given in Table 3. Observed and modeled mean days to various phenological stages generally are close together except for physiological maturity in the Texas data set. In most of the cases, the standard deviations are similar and residual mean square error values are small. The regression coefficients are close to unity in most of the cases.

Due to serial planting in three locations days to flowering varied. The regression is closer to the 1:1 line and the scatter of data points around the 1:1 line is minimal. The simulation result is similar to the Texas data set. Taken together with the statistics presented in Table 3, predicted days to PI agreed well with the observed values. Predicting PI accurately is important for predicting days to flowering and determining the total number of leaves (TLNO) produced. The TLNO in turn influences assimilate production through the leaf area index (LAI) and light interception. Data presented here indicate that the described model is capable of simulating phenological stages reasonably well.

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Chapter 14

THE SIMULATION OF PLANT DEVELOPMENT IN GOSSYM

Donald N. Baker and Juan A. Landivar

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I. INTRODUCTION

Cotton is an indeterminate fruiting woody perennial. However, it is usually cultured as an annual crop. Although it is often grown in humid areas of the world, cotton is usually classified as a xerophyte, and large commercial acreages occur in semiarid areas. The objective in the development of GOSSYM has been to provide farmers with a crop management decision aid and to provide to breeders and genetic engineers a tool for use in the computer-aided design of new and better adapted genotypes. Such a model would need to simulate cotton growth and yield in all areas, regardless of soil type or climate. This objective and the nature of the plant itself has required, among other things, a model of plant development that faithfully reflects not only that process, but related plant processes including growth, senescence and organ abortion. This, in turn, required a two dimensional spatial simulation of soil processes including heat transfer, water and salt movement, the mineralization of organic matter, and the soil nitrogen transformation processes. A comprehensive description of GOSSYM is provided elsewhere.[1] GOSSYM is a materials-balance model, driven by environmental inputs, in which nitrogen is assumed to be entrained in the transpiration stream and partitioned, along with photosynthate, to growing points on a daily basis. The model is subdivided into routines which deal with specific plant and soil processes. This has facilitated model development, including controlled environment studies to form the data base, and, due to the correspondence of rate functions and coefficients with some heritable traits, it has contributed to the use of the model in breeding feasibility studies.[2,3]

GOSSYM has been extensively validated against 57 crop years of data collected in Israel[4] and against over 100 commercially grown crops in all cotton producing areas of the U.S. The data sets from Israel compare seasonal time courses of measured and simulated numbers of squares, bolls, mainstem nodes, and weights of stems, bolls and leaves. The U.S. data sets deal only with yield. Mean yield prediction accuracy now approaches 90%.

We noted earlier[1] that the structure, strategy and content of crop simulation models is dictated mainly by the disciplinary background of the modeler and the modeling group, and that the impact of disciplinary background of the modeler on structure is often seen in the modeler's perception of the consequences of including or deleting certain mechanisms and in the data base that is likely to be available or which can be obtained on which to build the model. Much of what follows in this chapter flows from the fact that we had developed the soil-plant-atmosphere-research system (SPAR) specifically for the purpose of providing data bases for physiological process rates to the modeler constructing dynamic crop simulation models.[5] In this facility, continuous records of photosynthesis, respiration, transpiration, growth (including root growth), development and organ abscission are maintained.

The overall architecture of GOSSYM is presented in Figure 1, but this discussion focuses on the subroutines GROWTH, PLTMAP and ABSCISE, with references to subroutines simulating respiration, photosynthesis, root growth and nitrogen movement in the plant (PNET, RUTGRO and NITRO, respectively). These subroutines are called daily.

The PNET subroutine treats the crop canopy as an optical surface and calculates photosynthesis and respiration on a land area basis. Respiratory loss is subtracted from photosynthesis and the result is added to reserves left over from the growth of the previous day to form a carbohydrate pool available for growth in the current day. This pool and the nitrogen pool are divided by plant population so that growth and developmental processes are handled on an individual (average) plant basis.

II. SUBROUTINE GROWTH

This subroutine calculates potential and actual daily increments of growth of each of the organs on the plant. The data base is from phytotron experiments for the temperature responses

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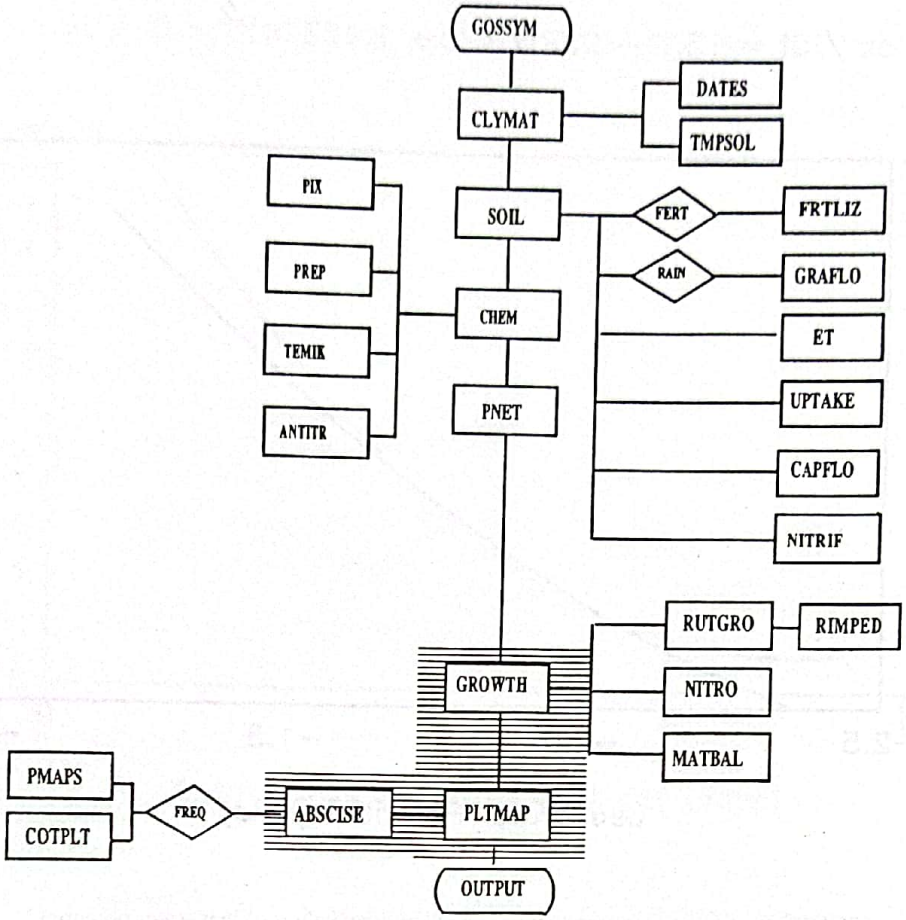

FIGURE 1. The overall architecture of GOSSYM.

and from SPAR experiments for water-stress responses. Growth of a particular organ is limited only by its developmental state, turgor, the concentration of the plant growth regulator, mepiquat chloride, (trade name PIX) and the supply of metabolites. It is not limited by specification of any maximum size. Root growth is calculated in a separate subroutine (RUTGRO), which is called twice from GROWTH to calculate first potential and then actual root dry matter accretion. In RUTGRO, the soil water potential in those parts of the profile containing roots is calculated for use, along with climate information, in calculating water-stress parameters.

Simulated growth strategy is as follows. The size and age of each organ on the plant is considered and the potential growth rate is calculated as a function of temperature, assuming no shortage of photosynthate or nitrogen. A total carbohydrate demand (CD) is calculated as the sum of potential growth increments of all the plant organs. Plant attributes used in this calculation include organ weights and ages (since initiation). Potential growth is calculated for day and night periods separately, using temperature and water-stress inputs appropriate to those time periods.

Potential stem weight growth for the first 35 days of the season is of the following form:

$$\text{PDSTMD} = (0.1 + 0.02 * \text{IDAY}) * \text{FACDAY} \qquad (1)$$

where PDSTMD is the potential change in weight of the stem during the daytime, and IDAY is the age of the plant. FACDAY is a combination of water stress and growth regulator (PIX) reduction factors. It is defined as follows:

$$\text{FACDAY} = \text{DAYTYM} * \text{AMIN}(1.0,\ \ 0.2 + \text{WSTSTD}) * 0.31 * \text{PIXDZ} \qquad (2)$$

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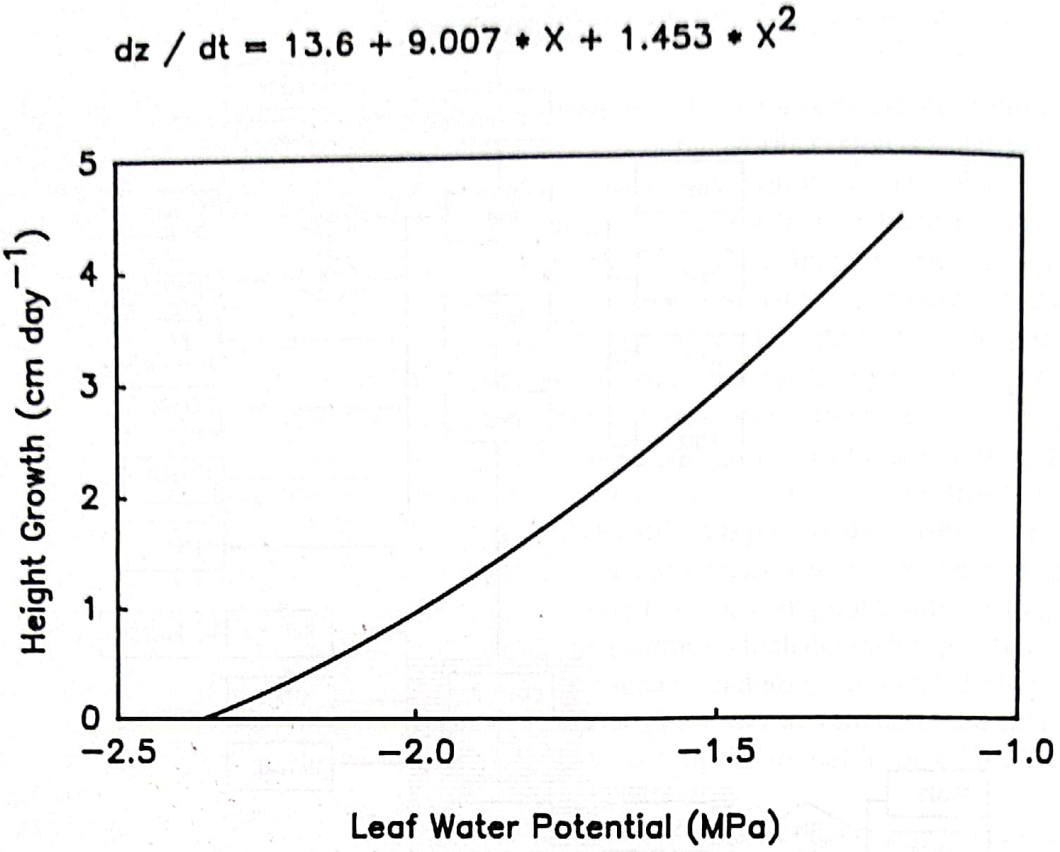

FIGURE 2. Growth rate of plant height vs. midday values of leaf water potential.[6]

where DAYTYM is the fraction of the 24-h period in daylight, WSTSTD is a water stress reduction factor developed from the data of Marani et al.,[6] and PIXDZ is a chemical growth regulator reduction factor derived from the data of Reddy et al.[7,8] This statement means that FACDAY is the product of DAYTYM times whichever is less, 1.0 or 0.2+WSTSTD, times 0.31 times PIXDZ. The multiplier 0.31 is a calibration factor which helps the model respond better during seedling growth. However, PIX is rarely used before first square and so the 0.31 multiplier rarely takes effect. The water-stress response data are presented in Figure 2. WSTSTD is the ratio of height growth (from Figure 2) at the calculated midday leaf water potential to that at full turgor. PIXDZ has values ranging from 0.5 to 1.0. It is based on calculated tissue concentration, which depends on application rate and the plant dry matter added since the application. After 35 d the 0.31 term is deleted from the FACDAY calculation and PDSTMD is calculated as follows:

$$\text{PDSTMD} = \left[0.2 + 0.06 * \left(\text{STEMWT} - \text{STMWT}(\text{IDAY} - 32)\right)\right] * \text{FACDAY} \qquad (3)$$

where STEMWT is the stem weight through yesterday and STMWT(IDAY–32) is the stem weight as of 32 d ago. The statement that stem growth is proportional to stem biomass accumulated in the past 32 d is justified on the basis of stem conversion to woody (dead — no longer capable of dry matter accretion) tissue.

At the time of the original development of GOSSYM, no phytotron data could be found which correctly predicted stem height growth rates in the field. The model was, therefore, based on field data.[9] In the model, stem height growth is based on the age of the top three nodes. Thus, simulated height growth is related to development rate, which was reliably obtained from controlled environment data in the literature and which, as will be seen later, is written as a function of

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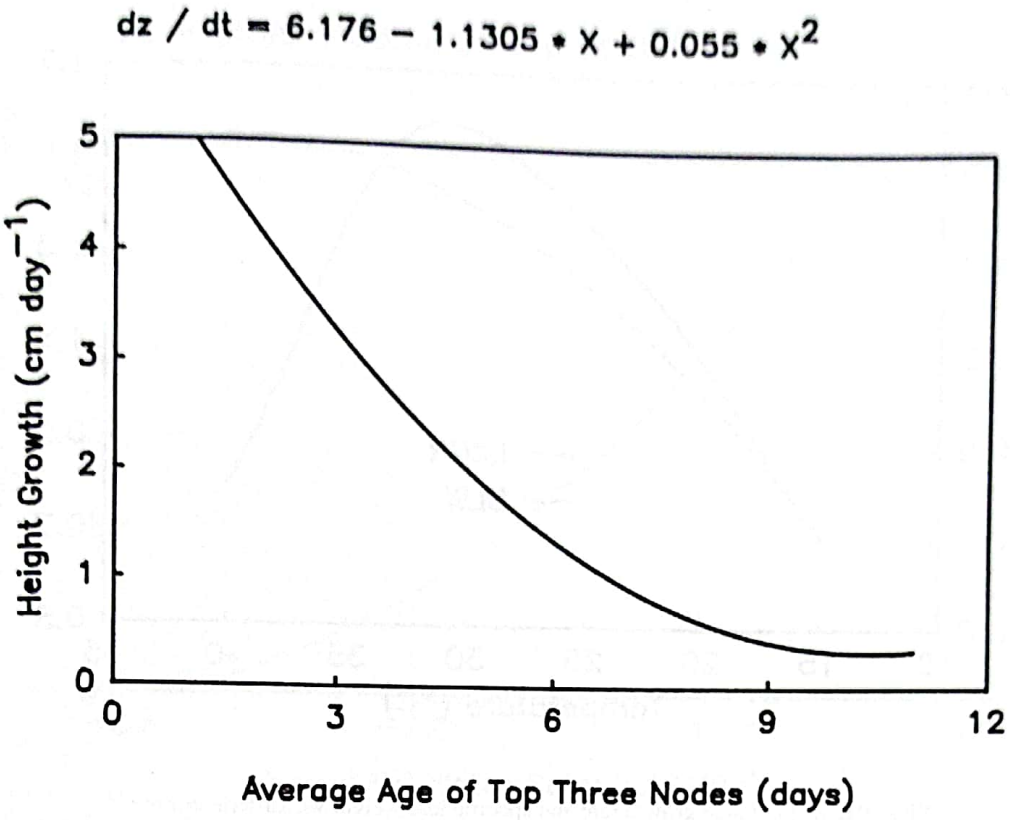

FIGURE 3. Daily stem height growth vs. average of top three nodes.[1]

temperature and metabolite supply. The initial estimate of height growth increment is subsequently modified by the water-stress and growth-regulator (PIX) reduction factors. The equation describing the data base for height growth is presented in Figure 3.

The potential leaf area growth and an associated estimate of specific weight for each leaf are calculated from temperature and then reduced by water-stress and PIX reduction factors. The specific leaf weight and the potential area growth increments are used to estimate a potential weight gain for each leaf. Graphical and mathematical representations of the data bases for potential leaf growth and for the effect of water stress on leaf area growth are presented in Figures 4 and 5, respectively. Leaf area growth is calculated first. This is then reduced by normalizing with the water-stress response function in Figure 5. Then, specific leaf weight is calculated from the data in Figure 4 and used to convert the potential leaf area growth increment into a leaf mass increment.

Root growth is calculated in a series of steps in each cell of a hypothetical 20×40 cell grid extending from one row to the next and 2 m deep. Physical-chemical properties and conditions in each of the cells are established before the season and maintained in several time steps per day. A materials balance of water, nitrogen and root biomass in three age categories is updated daily in each cell.[10] Then, in each cell of the root matrix, an estimate of potential growth is based on soil temperature and the biomass of roots in an age category capable of growth. The concept of an age dependency of water uptake and growth of roots is taken from Graham et al.[11] Second, potential root growth is reduced in areas of the matrix with a shortage of nitrogen. This makes additional carbohydrate available for root growth in grid positions with good nitrogen supplies. Third, based on the level of water stress in the plant and the ratio of root to stem plus leaf biomass, potential root growth may be increased. Finally, the direction of root growth from a parent cell to daughter cells in the root matrix is controlled by relative amounts of mechanical impedance in the various cells in which growth may occur.

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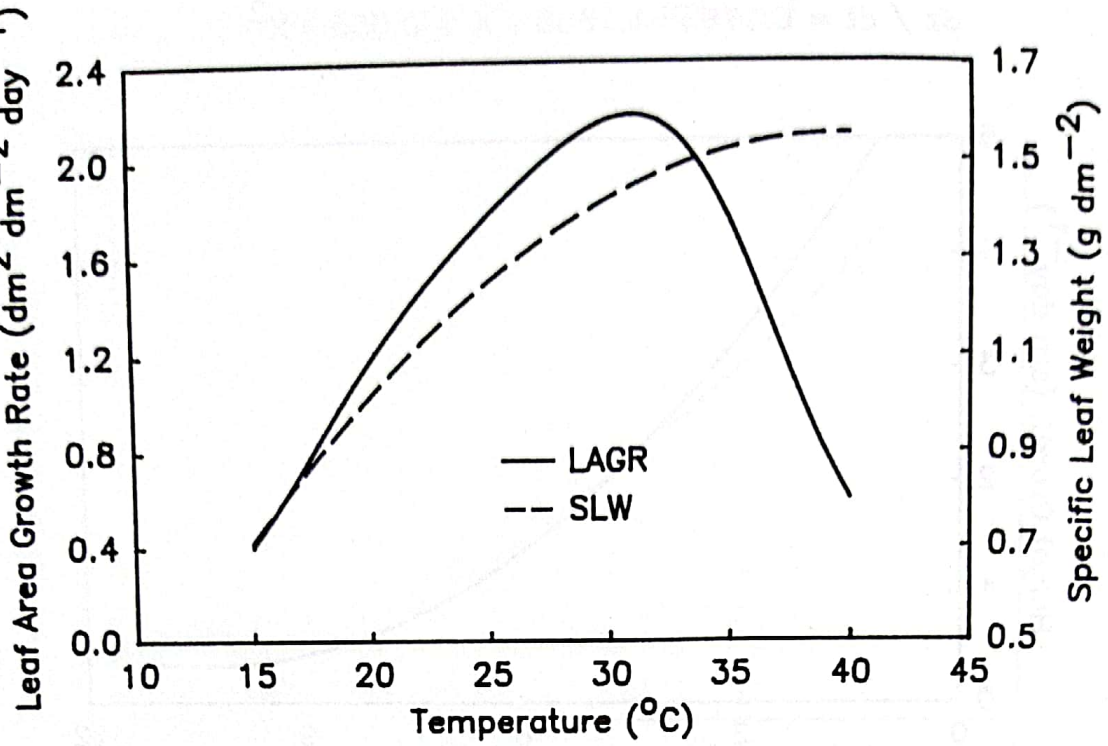

FIGURE 4. Leaf area growth rate and specific leaf weight vs. air temperature.[17]

Potential boll growth is calculated from temperature and adjusted downward under conditions of water stress. The temperature responses of boll growth presented in Figure 6 is from MacArthur et al.[12]

Following the calculation of potential carbohydrate requirements, the NITRO subroutine is called from GROWTH. NITRO estimates the nitrogen required for the assimilation of the amount of carbon just estimated for each of the organs. These nitrogen requirements are summed for the vegetative and fruiting parts, and the sums are used to estimate the total nitrogen requirement (demand) for that day. The nitrogen supply to the plant is estimated from reserves stored in leaf tissue plus nitrogen taken up during the day. Both active and passive uptake are calculated. The daily supply:demand ratio is calculated to estimate the maximum fraction of the potential carbohydrate that can actually be assimilated in above ground vegetation (NV), roots (NR) and fruiting (NF) organs, considering the nitrogen limitations. These fractions allow calculation of reduced or refined estimates of potential organ growth increments.

A carbohydrate supply:demand ratio is calculated as follows:

$$\text{CPOOL} = \text{PN} + \text{RESC} \tag{4}$$

$$\text{CSTRES} = \frac{\text{CPOOL}}{\text{CD}} \tag{5}$$

where CPOOL is the total available pool of carbohydrate from today's increment of photosynthate production (PN), plus reserve carbon (RESC) carried in from earlier days, CD is total plant carbohydrate demand and CSTRES is the carbohydrate supply:demand ratio.

Actual growth of each of the organs on the plant is then calculated as the product of potential growth of that organ multiplied by CSTRES. This partitions photosynthate to each organ on the plant purely on the basis of the contribution of that organ to the total demand. No preference is assumed in the allocation of dry matter on the basis of age or proximity to the photosynthetic sites. There is little debate in the literature over the existence of any limitation to growth resulting

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$$DL = 44.89 + 33.98\ LP + 6.38\ LP^2$$

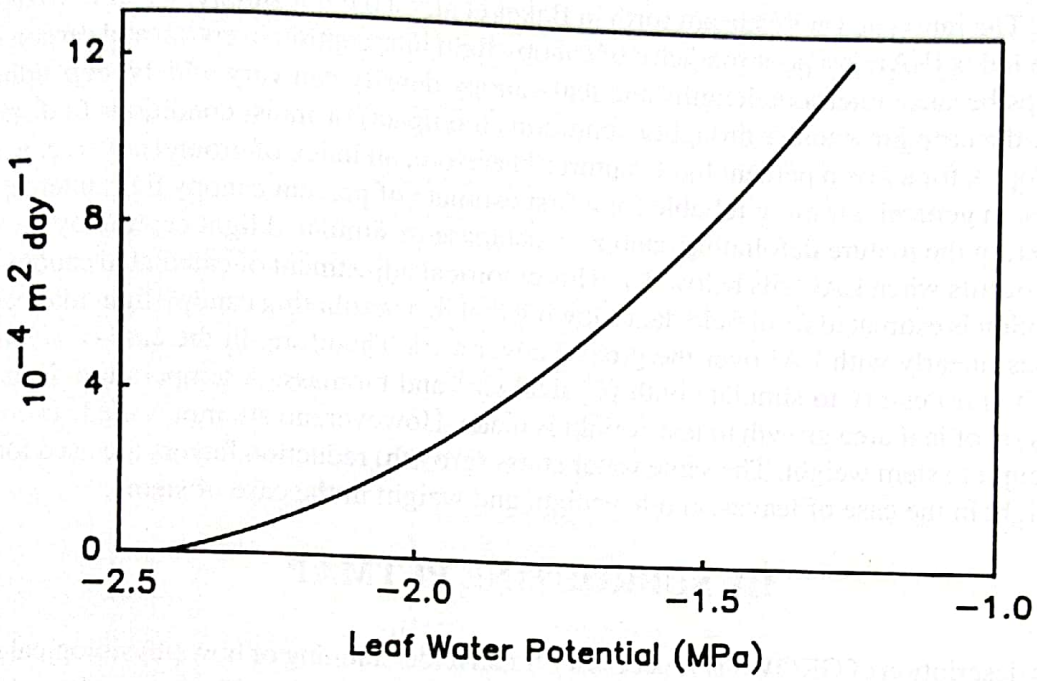

FIGURE 5. Leaf area growth rate vs. midday leaf water potential.[6]

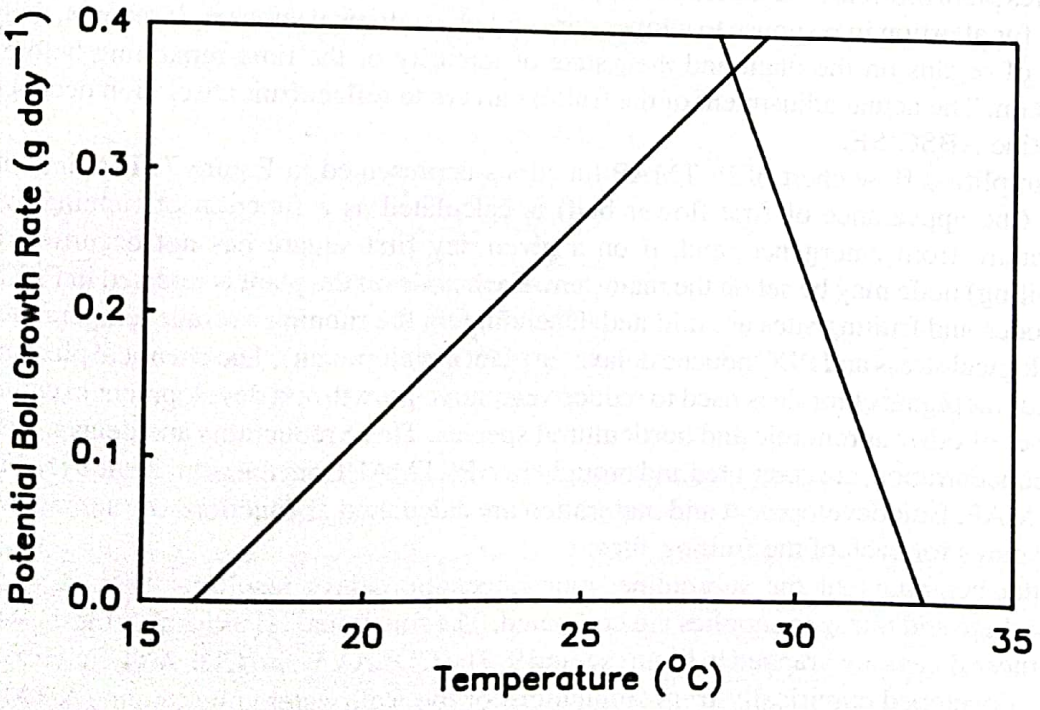

FIGURE 6. Boll growth rate vs. temperature. Values at 27° C and above were determined for plants in air enriched with CO_2 and with every other flower removed for some plants.[12]

from limitations in the translocation capacity of phloem elements in cotton. There is, however, some controversy over whether or not bolls should be given preference over other organs. We ourselves have been ambivalent on this. Our earlier model (SIMCOT II)[13] gave preference to boll growth for carbon allocation, and we have built an Acala GOSSYM[4] which does the same.

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NITRO, however, gives preference to the bolls over other above-ground vegetation in the allocation of available nitrogen.

Light capture, and therefore photosynthesis, depends primarily on plant height and row spacing. The rationale for this is put forth in Baker et al.[14] To put it simply, we have found that leaf area index (LAI) is a poor predictor of canopy light interception in cotton and certain other row crops because internode lengths and leaf canopy density can vary widely, depending on whether the crop grew under droughty conditions (compact) or moist conditions (a dispersed leaf canopy), for a given percent light capture. Therefore, an index of ground cover, e.g., plant height is, in general, far more reliable for a first estimate of percent canopy light interception. However, in the mature defoliating canopy, a decrease in simulated light capture by the plant canopy occurs when LAI falls below 3.1. This empirical adjustment of calculated canopy light interception is estimated from field data showing that in a defoliating canopy light interception decreases linearly with LAI over the ground cover area. Therefore, in the case of stems and leaves, it is necessary to simulate both physical size and biomass. A temperature-dependent conversion of leaf area growth to leaf weight is made. However, no attempt is made to convert plant height to stem weight. The same water stress (growth) reduction factors are used for area and weight in the case of leaves, and for height and weight in the case of stems.

III. SUBROUTINE PLTMAP

This description of GROWTH is necessary for an understanding of how physiological stress is defined and how it affects plant morphogenesis and fruit abscission. Those two physiological processes are treated in the subroutines PLTMAP and ABSCISE, respectively. PLTMAP simulates plant morphogenesis. It handles timing of plant morphological events and the marking of fruit for abortion in response to temperature and physiological stresses. It records, daily, the census of organs on the plant and their state of maturity or the time remaining before their abscission. The actual adjustment of the fruiting arrays to reflect fruit abscission occurs in the subroutine ABSCISE.

A simplified flow chart of PLTMAP functions is presented in Figure 7. The time of first square (the appearance of first flower bud) is calculated as a function of running average temperature from emergence, and, if on a given day first square has not occurred, a new (prefruiting) node may be set on the mainstem. Each node on the plant is updated in PLTMAP. New nodes and fruiting sites are initiated depending on the running average temperatures and physiological stress and PIX induced delays (in plant development). The chemical plant growth regulator mepiquat chloride is used to reduce vegetative growth and development in cotton and a number of other agronomic and horticultural species. These reductions and delays, based on tissue concentration, are computed and brought into PLTMAP from the subroutine PIX. Finally, in PLTMAP, fruit development and maturation are calculated as functions of running average temperatures for each of the fruiting sites.

At the beginning of the subroutine, morphogenetic delays resulting from shortages of carbohydrate and nitrogen supplies are computed. The functional relationships for the calculation of these delays are graphed in Figures 8 and 9. The CDLAYV and CDLAYF functions were initially developed empirically from simulations of the well-watered treatment (AAA) in the Bruce and Römkens[9] experiment in which high levels of nitrogen fertilization were used. We assumed that there were no nitrogen shortages in those plants. We proceeded to manually adjust the morphogenetic rates and the fruit abscission (further discussion of abscission takes place later in chapter) rates until we had a perfect simulation throughout the season. The discrepancies between morphogenetic rates predicted from the temperature functions alone and those observed by Bruce and Römkens as the fruit load developed were used to obtain the correct FSTRES values and to develop the relationships shown in Figure 8. The coefficients derived from the Bruce and Römkens data have since been slightly modified with data obtained from

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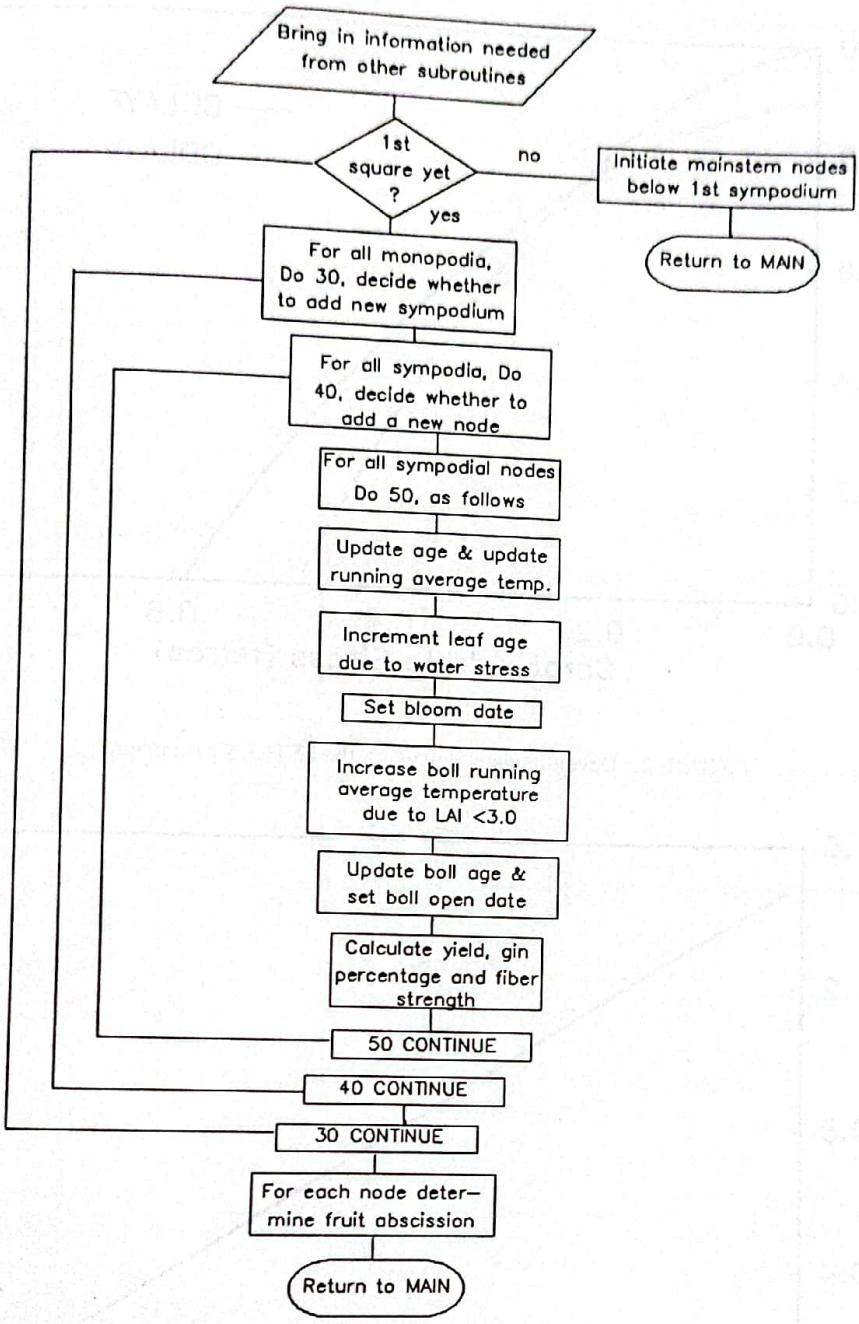
Bring in information needed from other subroutines
1st square yet ?
no
yes
Initiate mainstem nodes below 1st sympodium
Return to MAIN
For all monopodia, Do 30, decide whether to add new sympodium
For all sympodia, Do 40, decide whether to add a new node
For all sympodial nodes Do 50, as follows
Update age & update running average temp.
Increment leaf age due to water stress
Set bloom date
Increase boll running average temperature due to LAI <3.0
Update boll age & set boll open date
Calculate yield, gin percentage and fiber strength
50 CONTINUE
40 CONTINUE
30 CONTINUE
For each node determine fruit abscission
Return to MAIN

FIGURE 7. A simplified flow chart of PLTMAP functions.

modern varieties in well-fertilized field plantings. Nitrogen supply:demand ratios for fruit (NF) and vegetative (NV) growth are calculated with roots, fruit and other vegetative parts having first, second and third priorities, respectively. As suggested in Figure 9, NV is used to calculate delays in vegetative branch node formation. CSTRES is calculated in GROWTH as the supply:demand ratio for carbohydrates, and an overall metabolic stress term, FSTRES, is defined as the product of CSTRES and NF. Thus, prior to fruiting, NF will be 1.0 and FSTRES will equal CSTRES. We have attempted to calculate these demands in several other ways with poor results. The results suggest that some physiological change occurs in the plant at flowering which alters the physiological time between morphological events depending on the level of disparity between supply and demand for carbohydrates and amino acids in the plant. CDLAYV and CDLAYF (Figure 9) contribute to additional delays in node formation on vegetative branches and fruiting branches, respectively. After calculation of the physiological delays, if the first square has not yet appeared and there are not yet nine nodes on the mainstem, the formation

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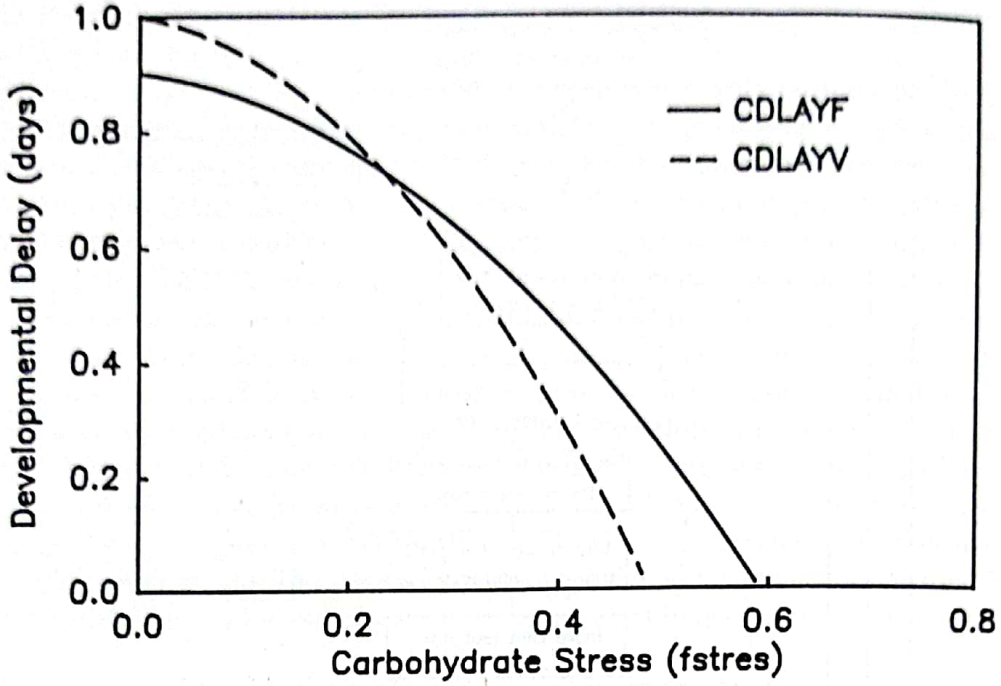

FIGURE 8. Developmental delays vs. the FSTRES parameter.[1]

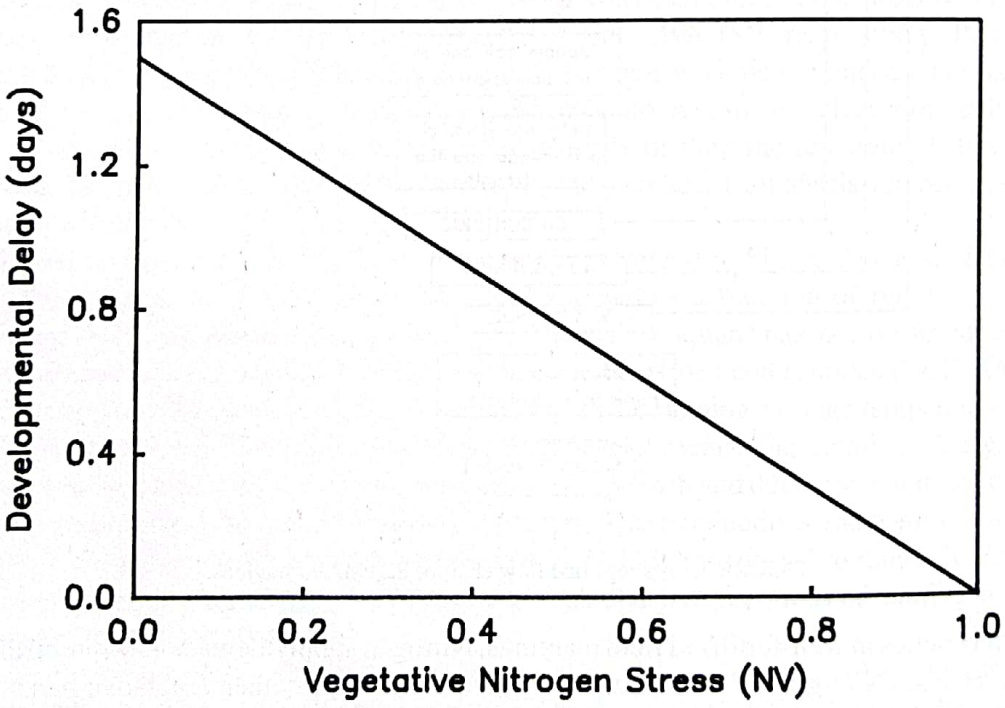

FIGURE 9. Developmental delay vs. the nitrogen stress parameter (NV).[1]

of further nodes proceeds. The time interval between mainstem nodes is a function of the running average air temperature since the last mainstem node appeared plus the stress-induced delays for the current day. The data for this functional relationship are taken from the phytotron experiments of Hesketh et al.[15] and are graphed in Figure 10. We have found that the time intervals between mainstem nodes in some modern cultivars are 50% shorter than in the cultivars used in the phytotron experiments, so a cultivar specific multiplier is attached to the regression equation summarizing those data. If sufficient time has elapsed since the last node was formed,

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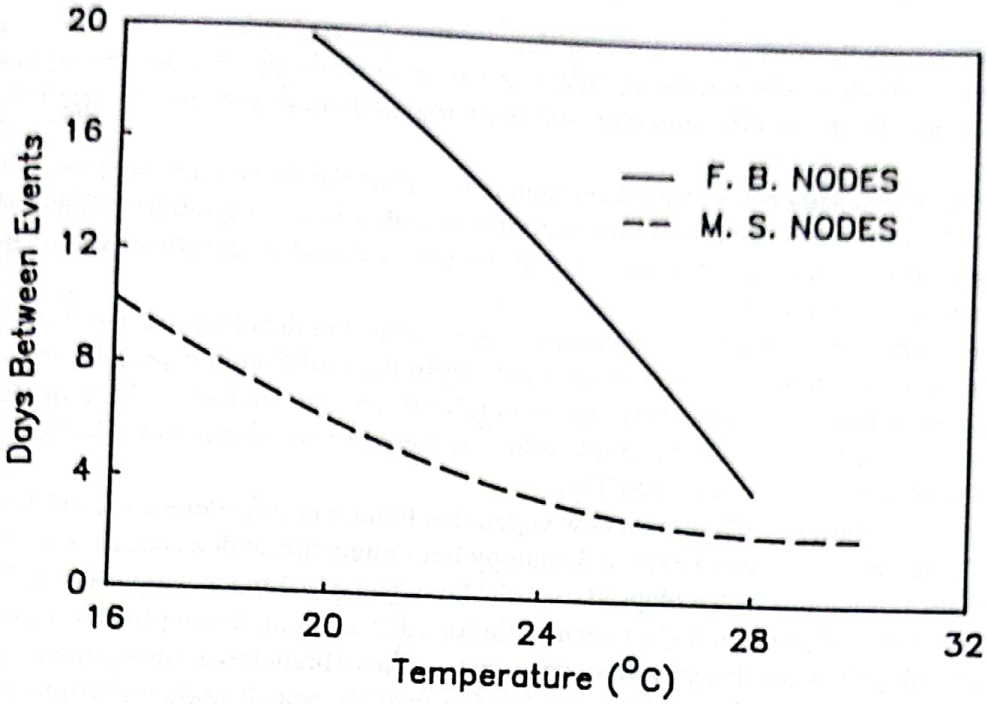

FIGURE 10. Time intervals between mainstem nodes and between fruiting branch nodes vs. temperature.[15]

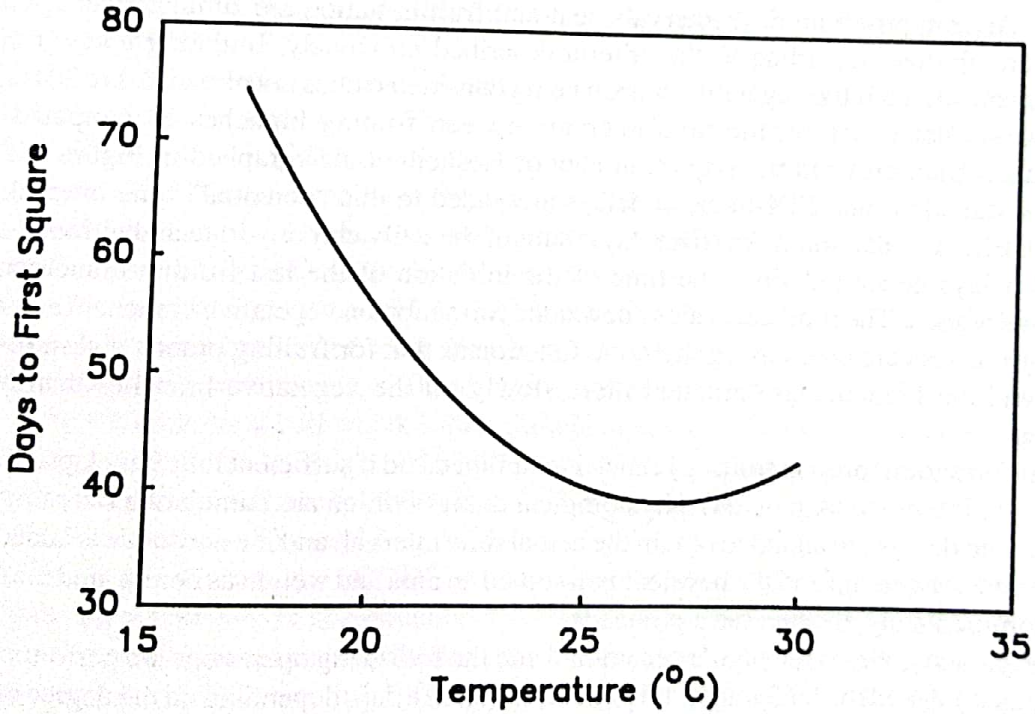

FIGURE 11. Time from emergence to first square in a Delta variety vs. temperature.[16]

a new node is formed with a leaf area initialized at 0.04 cm^2. The leaf weight is initialized using day and night weight factors (from GROWTH), and the weight is subtracted from the stem weight.

If first square has not yet occurred, the running average air temperature since emergence is updated. The time to first square is based on that value. The original data for this functional

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relationship are graphed in Figure 11. These data are from Moraghan et al.[16] The cotton in those phytotron experiments required about 20% more time to reach first square than do modern varieties in the field, so the equations summarizing their data contain a variety-specific multiplier.

If the day of first square has arrived, the square is set and the first elements of several three-dimensional arrays corresponding to monopodium number (K), sympodium number (L) and fruiting-branch node number (M) are set, and the time interval to the formation of the next mainstem node is estimated.

Next, if a plant bug population is believed to be present, a pinhead square loss is calculated. Some infestation of these insects is usually present in the mid-South, especially in the early season. We found from analysis of the Bruce and Römkens[9] data that about 4.6% of the newly formed squares will be lost, probably due to injury by these insects. Simulation of actual removal of the pinhead square occurs in ABSCISE.

Next, the possibility of initiating a new vegetative branch is considered. This is done if the number already present doesn't exceed 3, canopy light interception does not exceed 90%, and sufficient physiological time has elapsed since the last vegetative branch was initiated. This time interval is calculated as the time between initiation of mainstem nodes plus the time to first square (assuming the same delay from squaring on vegetative branches as on the mainstem), plus the physiological delays. If a branch is initiated, a fruiting branch node and fruiting site are initiated at the same time, and the appropriate codes are set up as before (setting first square). Further, if a new vegetative branch, and with it a new fruiting branch and fruiting branch node, is formed, a new leaf is initiated as before when the first square was formed.

Then, the logic for the formation of new fruiting branch and vegetative branch nodes is initiated. After appropriate time intervals, leaf and fruit initiation are simulated and pinhead squares are aborted according to the criteria described previously. Initiating a new fruiting branch is considered if the vegetative branch being considered does not already have 30 fruiting branches. As noted before, the time interval between fruiting branches is computed as a temperature function from the phytotron data of Hesketh et al.[15] graphed in Figure 10. Any physiological stress and PIX-induced delays are added to this "potential" time interval. The delay VDELAY is a cumulative (over days) sum of the daily carbohydrate and nitrogen stress induced delays generated since the time of the initiation of the last fruiting branch on this vegetative branch. The time interval for new node formation on vegetative branches (other than the mainstem) is calculated using the same function as that for fruiting branch nodes. In other words, fruiting branches are initiated more slowly on the vegetative branches than on the mainstem.

The information for each fruiting branch is examined and if sufficient time has elapsed, a new fruiting site is formed. Again, any physiological delays (which are cumulative over time) and PIX-induced delays are added to obtain the actual time interval, and if a new node is added, fruit and leaf codes are set up and the new leaf is assigned an area and weight as before, and the square may be immediately aborted (as a pinhead).

Finally, each node on the plant is examined and the following operations are performed. The node is aged 1 d, and the leaf is aged 1 d plus a fraction of a day, depending on the degree of water or nitrogen stress. Next, average temperatures of the node and the boll, if present, are updated. If LAI is less than 3.0, 5°C is added to the day temperature in estimating running average boll temperature to account for radiant heating.

If a fruiting structure is present, the following operations are performed, depending on its stage of development. Time from square to bloom is calculated. The data base for estimating time from square initiation to bloom as a function of temperature is presented in Figure 12. If sufficient time has elapsed for this square to bloom, boll growth is initiated. Rain is assumed to interfere with pollination. The bloom aborts if more than 12 mm of rain occurred on the day of bloom. The actual simulated loss is implemented by adding to the accumulated pollination loss

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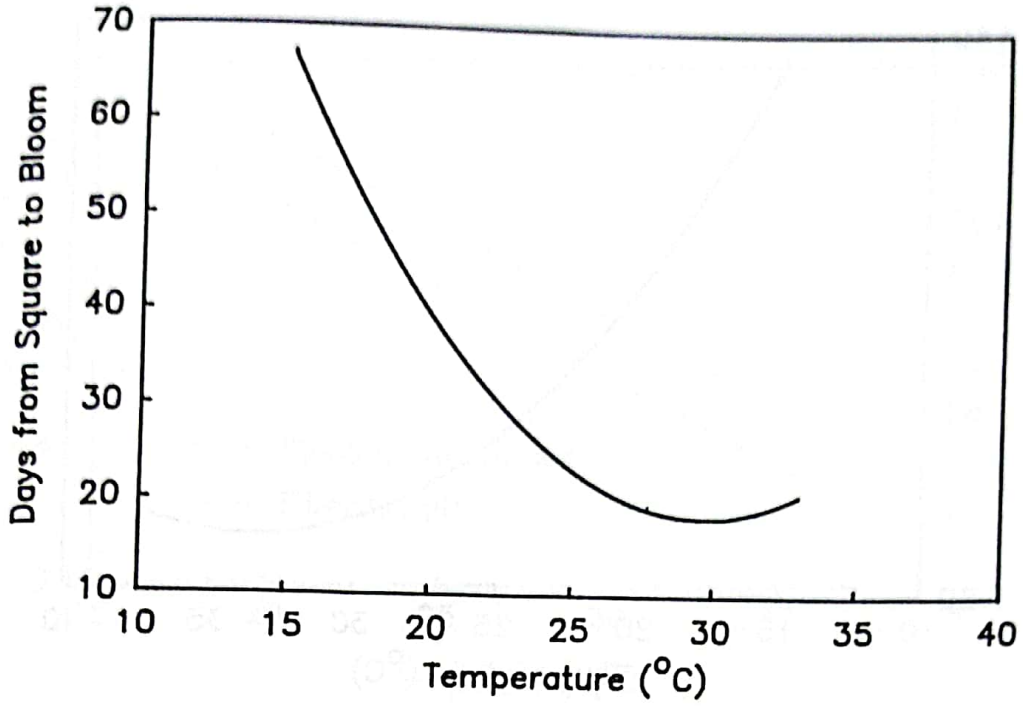

FIGURE 12. Days from square initiation to bloom vs. temperature.[17]

the fraction of fruit actually remaining at this particular site. If the accumulated POLOSS is greater than one, it is set equal to one. In other words, not more than one bloom per plant per day can be lost in this way.

If, however, this loss due to rain does not occur, the fruit remains on the plant and is counted among the green bolls on the plant. The simulated fruit code is set to seven indicating a green boll. The boll weight is initialized at 31% of the square weight at that site, to allow for weight loss in the corolla. The green boll weight is added to the cumulative green boll weight for the plant as a whole. If some green boll weight has accumulated on the plant, the date (FBLOOM) is recorded. Then the square weight for this site is set to 0.

Next, a running average of the FSTRES (product of supply:demand ratios for carbohydrate and nitrogen) values experienced since initiation of this boll is calculated, or updated. This is used to calculate the maximum age (limit) beyond which this boll may not be aborted due to stress. If the site contains a boll which is past the age of susceptibility to abscission (e.g., 15 d), the FCODE is set to 2. Next, the age of the boll at opening is calculated from the running average boll temperature. The data base for this temperature response also was taken from Hesketh and Low[17] and is presented in Figure 13.

If the boll is due to open, the FCODE is set to three to reflect this. The weight of the boll is added to the open boll weight accumulator, the weight is subtracted from the total plant green weight, and the nitrogen contained in the boll is subtracted from the total plant green boll nitrogen amount. At boll opening, fiber percentage, fiber length, and fiber strength are calculated from temperature functions published by Hesketh and Low[17] (Figures 14 to 16). Yield is calculated as the cumulative (over all bolls opened to date) weight of lint on the plant. It is expressed in terms of 500 lb bales per acre.

IV. SUBROUTINE ABSCISE

Leaf and fruit abscission are simulated in this subroutine. Leaf abscission occurs in response to senescence and fruit abscission in response to metabolic stress.

Leaf area and leaf biomass are used in other parts of GOSSYM in the following ways. When

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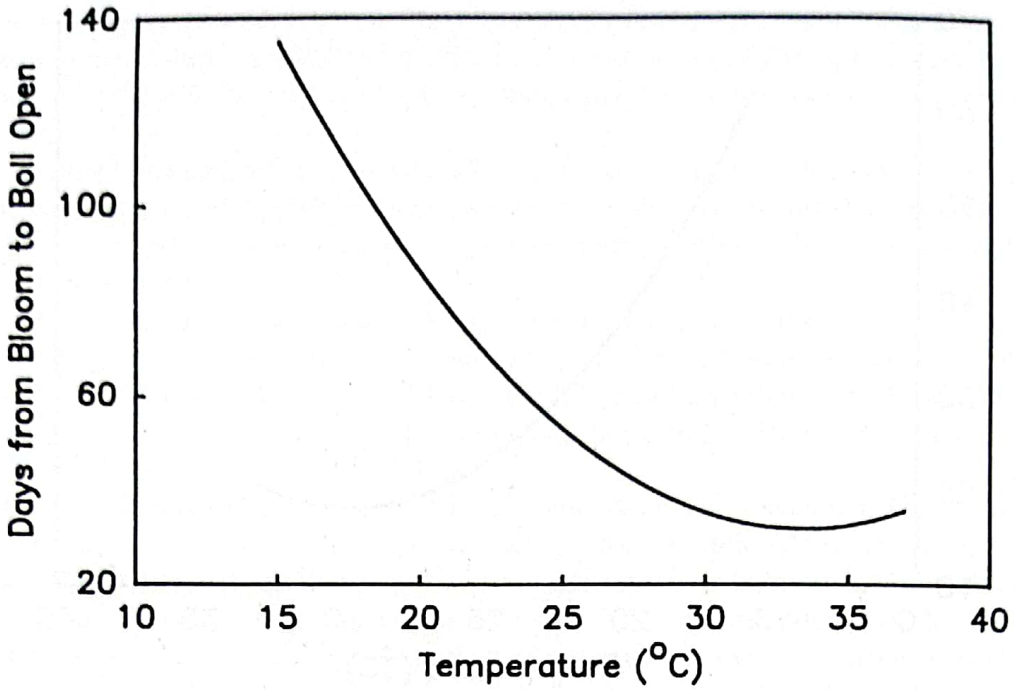

FIGURE 13. Days from bloom to boll open vs. temperature.[17]

LAI falls below 3.1, canopy light interception, transpiration, and photosynthesis are reduced.[18] Potential carbohydrate reserves are estimated as a fraction (up to 30%) of leaf biomass. Part of the nitrogen reserve is located in the leaves. The model contains the simple hypothesis that an abscising leaf has a nitrogen concentration of 1%. Moreover, the action of the growth regulator mepiquat chloride (PIX) is based on tissue concentration, and when a leaf is abscised some of the growth regulator is lost. Therefore, over time, as new (simulated) organs are formed and existing organs are lost, the PIX concentration and its effect on the plant decline.

The remainder of ABSCISE is devoted to the abscision of fruit on the plant. The data base for this function was developed from the plant maps obtained by Bruce and Römkens[19] in their AAA (well-watered) treatment, and from validation efforts such as those of Fye et al.[20] Cotton physiologists and agronomists have known for many years that several kinds of physiological stresses, including carbohydrate and nitrogen shortages and water stress, are associated with the "natural" abscission of squares and bolls. This area, including its hormonal aspects, has been the subject of much of the physiological research conducted over the last 30 years. However, very little is known about the linkages between the metabolic pathways and the hormone systems involved in abscission, and to this day, there is no model which describes this system explicitly and mechanistically. However, the simulation models, including GOSSYM and SIMCOT II, shed some light on the nature of fruit abscission, and what is now known appears to be applicable to other plant species as well.

The model description of abscission and the development of metabolic delays in fruiting began, historically, with our calculation of daily photosynthate production, respiration loss, and nitrogen uptake[21] as described previously. We then moved to examine the classical "nutritional theory". We theorize that hormone balances in the plant shift in response to some (mathematical) combination of both supply and demand for metabolites. We use the supply:demand ratio. These shifts result in lengthening or shortening time variables, such as plastochrons, and they result in the abscission of some fruit. In GOSSYM, we have written functional relations for this (described previously for the delays and later for abscission).

A good simulation of morphogenesis, fruiting, and fruit abscission was first obtained with Bruce and Römkens'[9] well-watered treatment, in which the relationships between morphogenetic delays and the physiological stress parameters and between fruit abscission and the stress

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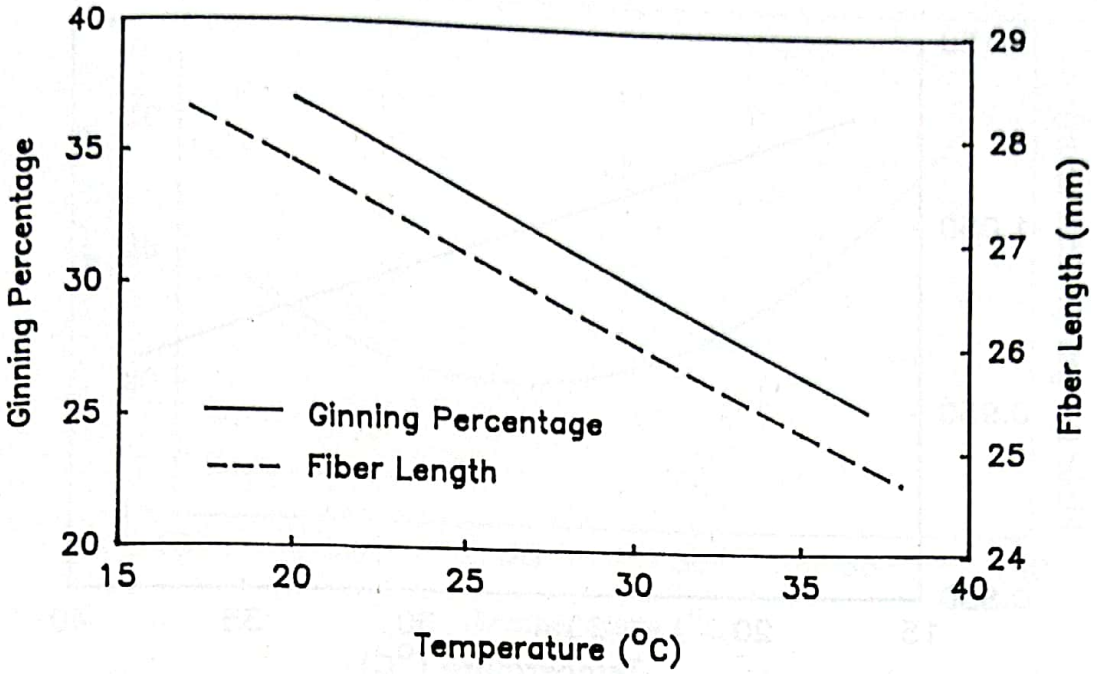

FIGURE 14. Effect of temperature on gin percentage and fiber length in several cultivars.[17]

parameter FSTRES were manually adjusted. This procedure provided FSTRES values appropriate to the amount of abscission (in that case). Different relationships are used for plants with fruit dry weight:total plant dry weight ratios above and below 0.05. These relationships are graphed in Figure 16.

GOSSYM simulates the effects of water stress on fruiting entirely within the framework of the nutritional theory. The first step is computation from these functions of the total number of fruit to be lost from the whole plant. Then, the actual simulation of the fruit abscission process begins. The model permits the abscission of partial fruit at each site containing squares or bolls in the susceptible age categories. For squares, the age range is 2 to 30 d. As noted, for bolls the age range depends on stress level. Therefore, the first step is to compute the fraction of each of today's squares and bolls to be removed. These fruiting structures will actually abort 7 d from now. The fruit to be abscised today were marked for abscission as a result of stress occurring 7 d ago (plus today's pinhead and pollination losses). Thus, the fraction of each of the squares and bolls to be removed today is defined as the number of squares and bolls marked 7 d ago divided by the sums of squares and bolls on the plant today. However, the square fraction is limited to a maximum of (DPSMX=) 0.5. Next, the number of blooms produced in the past 7 d is calculated and those which have bloomed are shed as bolls rather than as squares. Square loss is therefore calculated as the number of squares marked for abscission 7 d ago, minus those which have become blooms, plus the pinhead squares that have been marked during the current day. Bolls to be lost today equal the number of bolls marked for abscission 7 d ago, plus the blooms whose petals have been stuck by rain, plus the marked squares which have become bolls in the past 7 d. The fraction of existing susceptible bolls to be dropped is not allowed to exceed the limit (DPBMX) 0.3.

If the program attempts to drop more bolls than exist, the fraction of susceptible bolls to be lost is set to 1.0, and the square loss is recomputed to make up the difference to provide the same total fruit loss. Similarly, if the program attempts to drop more squares than exist at this time, the boll loss is redefined so that the excess square loss is made up as boll loss. Again, the fractional limits are preserved.

Finally, the actual removal of the fruit from the plant is done. If the fruit is a square and it is

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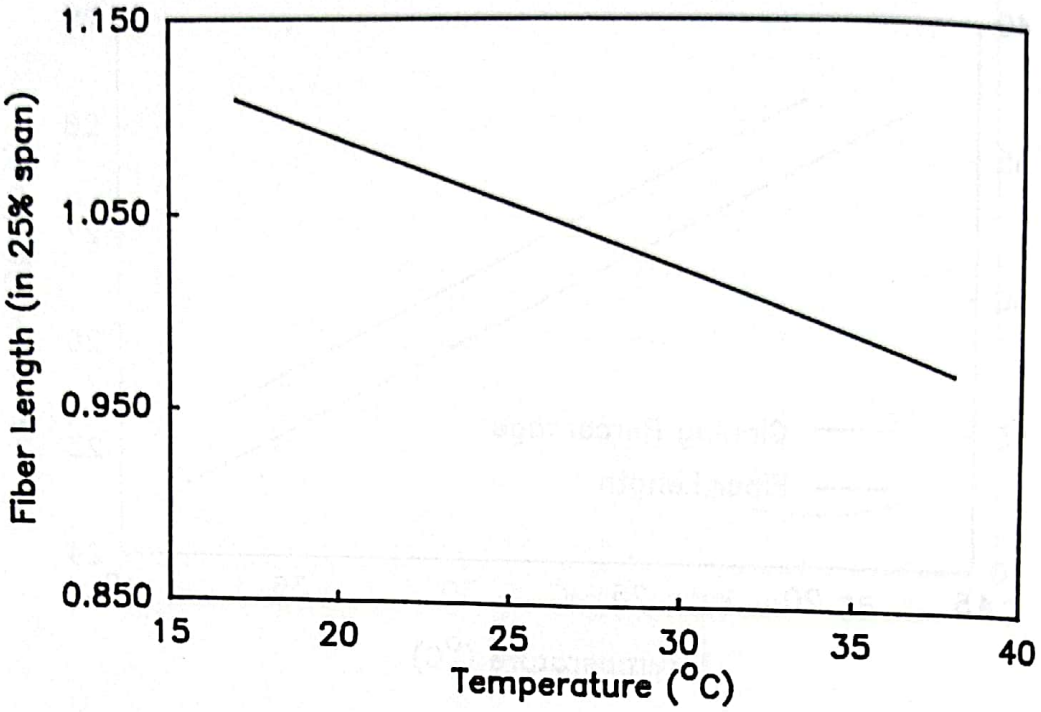

FIGURE 15. Effect of temperature on fiber strength.[17] Fiber strength is stated in terms of g tex^{-1}, where tex is a bundle consisting of 1000 m of fibers, so the strength is the grams force required to break a fiber bundle 1 tex in size.

between 4 and 30 d old it is susceptible, and a fraction (FDROPS) of it will be dropped. Fruit numbers and weights are removed from the appropriate registers and added to registers representing cumulative losses.

Similarly, green boll numbers are summed, and if the boll age is less than the susceptible boll age limit, a fraction (FDROPB) of the fruit at that site is dropped. Again, this involves removing the fruit numbers and weights from the appropriate registers and adding the losses to other registers to keep records of cumulative boll losses. In the case of boll losses, a record is also kept of tissue nitrogen losses.

V. SUMMARY

This chapter describes a model of cotton growth and development. It defines stress as a metabolite source:sink imbalance capable of shifting hormone balances within the plant and causing the abortion of fruit and delaying plant development. Little if any photoperiodic response occurs in commercially grown cotton and the logic described here results in, or simulates, the sigmoid growth and developmental patterns exhibited by this indeterminant fruiting woody perennial. The objectives of environmental impact assessments, breeding feasibility and design studies, and farm level applications over the entire range of soils and climates experienced by the crop mandate both a strict adherence to process level physiology in structuring the model and a controlled environment data base for the formulation of rate functions. This chapter describes some of the model structure and the data base. The model has been validated against approximately 200 field crops and it is being used for crop management decision making on about 60 farms.

In implementing this model, the first step is to calculate the potential growth of each of the organs on the plant. These calculations take into account the effects of temperature, tissue turgor, and plant growth regulators. The second step is to form the supply:demand ratios for carbohydrate and nitrogen. These ratios are used for dry matter partitioning and as indices of

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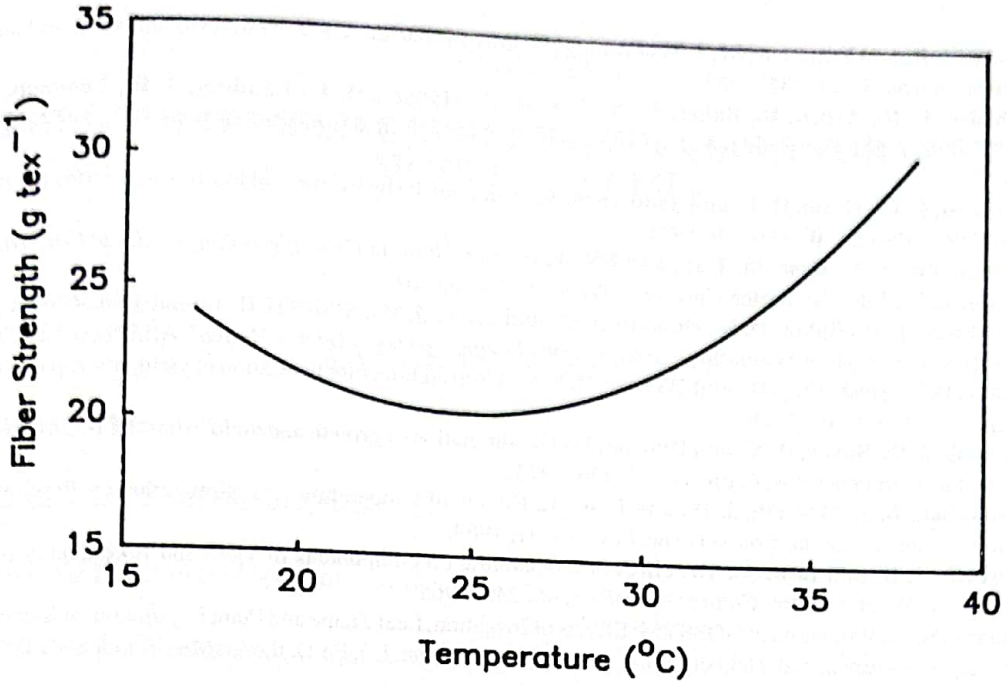

FIGURE 16. Numbers of fruit lost vs. FSTRES for plants with fruit dry/total plant dry weight ratios above and below 0.1.[1]

developmental delays and fruit abscission. Height growth is linked to temperature and all of the factors affecting plant development, since it is calculated from the average age of the top three nodes. In partitioning limited carbohydrate supplies no preference is given to fruit; however, if nitrogen is limiting, some preference is given to roots and then to fruit. The third step is to partition the daily increment of dry matter and to record the formation of new nodes, organs, etc. The last step is to tag fruit for abscission 7 d hence and to remove those tagged 7 d ago. The number of fruit tagged each day (FLOSS) is calculated from the stress value FSTRES of that day, which is defined as the cross product of the carbohydrate and nitrogen supply:demand ratios.

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Chapter 15

SIMULATING YIELD DEVELOPMENT USING THE COTTON MODEL *COTTAM*

B. S. Jackson

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I. INTRODUCTION

Phenological development in crop plants is often interpreted from the timing of yield development for the crop as a whole. In many determinant crop species, identifiable phenological events occur within a short time interval. For example, typically all of the viable grain embryos in sorghum will reach anthesis within a period of approximately 4 d.[1] In cotton, however, yield is comprised of a number of fruits that develop independently and may flower over a period in excess of 5 weeks.[2-4] Thus, in cotton, the distinction must be made between the phenological development of the individual fruit and the development of yield for the whole crop.

This chapter describes the phenological development algorithms used in the cotton plant model COTTAM.[5] COTTAM is a mechanistic model in which growth processes are described empirically. Thus, phenological stages are based on observational data rather that exact physiological definitions. For example, "square appearance" is defined from a square with 3 mm wide bracts. At that stage of development, three or four additional squares may be found if the primordia is dissected.[6] Similarly, boll maturity is defined from when the boll carpels split, while boll growth is known to cease 7 to 10 d earlier.[7,8]

In the first section of this chapter, phenological development of individual cotton fruit is described. The second section covers the integration of individual fruit into development of a whole plant. In the final section, the resulting fruiting model is demonstrated.

II. INDIVIDUAL FRUIT DEVELOPMENT

The stem structure of the cotton plant is shown in Figure 1. It consists of a main vertical stem on which nodes develop at regular intervals.[9] Between nodes five and nine, the cotton plant initiates a fruiting branch (sympodia) on which fruiting sites (fruit nodes) and squares appear. Fruiting branches appear on all succeeding mainstem nodes as well. The appearance of the mainstem node of the first fruiting branch (MSNo) is assumed to coincide with the appearance of the first square. Thus, the appearance of the first fruiting branch initiates the fruiting cycle in cotton.

In the absence of a fruit load or environmental stress, the interval for mainstem node appearance (plastochron) is approximately 40 heat units calculated from a base temperature of 12°C.[10-12] The rate of hypocotyl elongation also has a base temperature of approximately 12°C.[13] Thus, the period of development from sowing to first square appearance can be taken as one continuous period. Constable[14] showed that a constant of 450 heat units (corrected to 12°C) approximately described the period from sowing to first square appearance for 30 serial sowings over a 3-year period. The MSNo may vary with cotton cultivar.[15-17] Therefore, the period from sowing to first square appearance may be approximated as 330 heat units for an early cultivar, 390 heat units for an intermediate cultivar, and 450 heat units for a late-maturing cultivar.

The period from sowing to first square appearance has also been shown to be influenced by a number of environmental factors other than temperature. Of these, the effects of cool temperatures and water deficits occur most frequently. Wanjura et al.[13] reported that temperatures below 11°C would delay emergence. Water stress will also delay emergence and stem elongation.[18,19] When predicting first square appearance, these factors must also be taken into account. The period from sowing to first square has also been shown to be influenced by long daylengths and excessively high temperatures.[12,15] However, normal planting times will usually preclude these conditions.

After appearance of the first square, successive squares appear. However, the appearance rate of these squares is dependent on other characteristics of morphological development of the cotton plant and is discussed in following sections.

Square period, that period between square appearance and flowering, can be defined in terms

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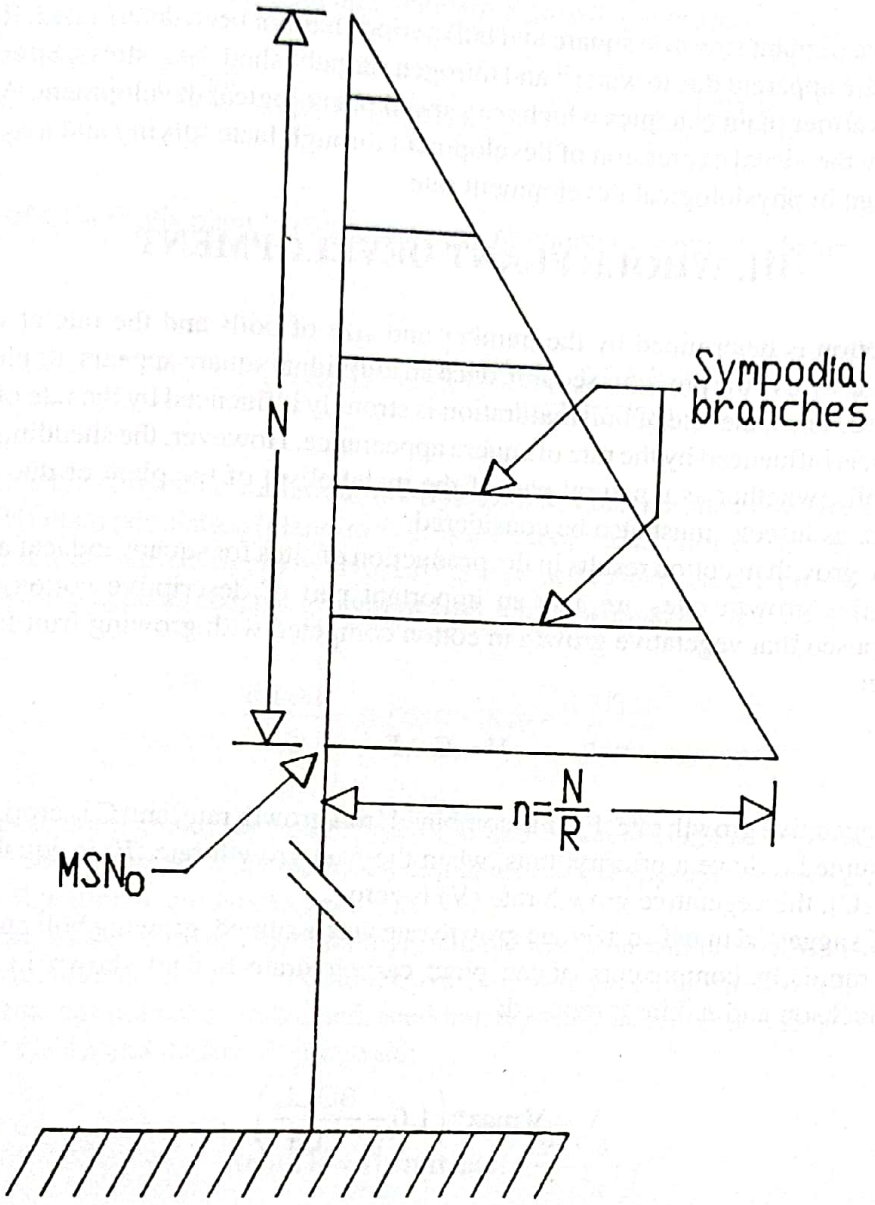

FIGURE 1. Conceptual cotton plant showing mainstem nodes (N) above the MSNo and subtending sympodial branches. The number of fruiting sites on a sympodial branch (n) is proportional to the number of mainstem nodes above it by the factor R.

of heat units. The data of Hesketh et al.[10] indicate a square period of 392 heat units. Young et al.[20] reported a range of 264 to 354 heat units for several sowing dates averaged for 2 years. Hesketh and Low[21] showed no differences in square periods among three diverse varieties of cotton. The reported duration of square period is dependent on the criteria for identifying square appearance. In COTTAM, appearance is determined from a 3 mm wide square, and a square period of 380 heat units is used.

Boll period, that period from flowering to opening of the boll, can be described as an exponential function of the average temperature. Wanjura and Newton[8] reported:

$$\text{BPER} = 548.0 * \exp(-0.0903 * \text{TBAR})$$

where BPER is the boll period (days) and TBAR is the average temperature for the boll period (C). Mutsaers[7] and Jackson and Arkin[11] showed varietal differences in boll periods of between 3 and 5 d. However, for the modeling exercise at hand, these differences are ignored.

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The influence of plant stress on square and boll periods has not been determined. Reductions in boll periods are apparent due to water[22] and nitrogen (unpublished data) stress. Stressed plants may result in warmer plant canopies which may speed phenological development. Also, stress may speed only the visual expression of development through faster drying and may not cause an actual change in physiological development rate.

III. WHOLE PLANT DEVELOPMENT

Yield in cotton is determined by the number and size of bolls and the rate at which they mature. As described in the previous section, once an individual square appears, its phenological clock is defined. Thus, the rate of boll maturation is strongly influenced by the rate of flowering which, in turn, is influenced by the rate of square appearance. However, the shedding of squares and young bolls, whether as a natural part of the metabolism of the plant or due to external pressures such as insects, must also be considered.

Vegetative growth in cotton results in the production of sites for square and leaf appearance. Thus, vegetative growth rates are also an important part of descriptive cotton phenology. Mason[23] proposed that vegetative growth in cotton competed with growing fruit for available carbohydrate:

$$V = C - F \tag{1}$$

where V is vegetative growth rate, F is the combined fruit growth rate, and C is crop growth rate. Fruit are assumed to have a priority; thus, when the fruit growth rate (F) is equal to the crop growth rate (C), the vegetative growth rate (V) is zero.

Hearn[24,25] suggested that if an average growth rate was assumed, growing boll numbers could be used to represent components of the plant carbohydrate budget shown in Equation 1. Therefore, Jackson and Arkin[26] proposed:

$$V = V\,max * \left(1.0 - \frac{BOLL}{CCa}\right) \tag{2}$$

where BOLL is the number of growing bolls plant^{-1} and CCa is the carrying capacity defined as the number of growing bolls equivalent to the crop growth rate.

Hearn and da Roza[27] proposed defining vegetative growth rates in cotton from a conceptual plant model, as shown in Figure 1. Above the MSNo there are N mainstem nodes, each with a sympodial branch. In the absence of boll load or environmental stress, Jackson and Arkin[26] showed that the rate of fruiting site production could be represented:

$$\frac{d\,SITE}{d\,tp} = AA * SITE^{\frac{1}{2}} \tag{3}$$

where SITE is the number of fruiting sites plant^{-1}, tp is the time represented as accumulated heat units, and AA is a constant. Jackson and Arkin[11] reported values of AA that ranged between 0.0250 and 0.0308. Jackson et al.[5] placed an upper limit on the rate with which fruiting sites could develop that depended on plant population. For example, for a population of 14 plant m:

$$\frac{d\,SITE}{d\,tp} < AA * 5.0$$

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The relationship between boll load and vegetative growth becomes:

$$\frac{\text{d SITE}}{\text{d tp}} = AA * \min(\text{SITE}, 25.0)^{\frac{1}{2}} * \left(1.0 - \frac{\text{BOLL}}{\text{CCa}}\right) \quad (4)$$

The value of CCa (bolls plant^{-1}) changes as environmental conditions change. Jackson et al.[5] proposed:

$$\text{CCa} = \text{RAD} * 0.88 * \left(\frac{\exp(-\text{K} * \text{LAI})}{\text{BSZE} * \text{POP}}\right) \quad (5)$$

where RAD is the daily solar radiation flux (ly), BSZE is the assumed boll size (g seed-cotton boll^{-1}), POP is plant population (plants m^{-2}), K is the canopy extinction coefficient (e.g., 0.4) and LAI is the leaf area index. Prior to MSNo, LAI is assumed to increase at a rate of 0.012 per heat unit. After MSNo appearance, the growth of LAI is proportional to the growth rate of fruiting sites:

$$\frac{\text{d LAI}}{\text{d tp}} = 0.0080 * \text{POP} * \frac{\text{d SITE}}{\text{d tp}} \quad (6)$$

(leaf senescence is computed separately based soil water content). Other environmental stresses such water or nutrient stress must be added to Equation 4 where appropriate (for a more complete treatment of Equation 4 see Jackson et al.[5]).

As a characteristic of its indeterminant growth habit, cotton will normally shed some of its developing squares and bolls.[23,25,28] Although a direct link between square and boll shedding and crop growth rate has not been established, shedding typically increases as stress[28,29] or boll load increases.[30,31] Hearn and da Roza[27] proposed:

$$\text{SRATE} = f\left(\text{fruit age}, \quad \frac{\text{BOLL}}{\text{CCa}}\right)$$

where SRATE is the age-dependent shedding rate of young bolls and squares and f( ) is some function that increases with BOLL.

Experimental evidence suggests that the functional form of f( ) may be linear.[30] However, the growth of bolls is slow during the period 7 to 10 d after flowering, and bolls can be shed at any time during that period.[31,32] Lieth et al.[31] developed a description of shedding rates as a function of phenological age and the ratio BOLL/CCa. For example, the daily shedding rate of young bolls (less than 7 d old) may be approximated:

$$\text{SRATE} = \left[1.0 - \left(1.0 - \frac{\text{BOLL}}{\text{CCa}}\right)^{\frac{1}{7}}\right] \quad (7)$$

Equations 4, 5, and 7 describe the fruiting dynamics of the cotton plant, but they are incomplete. Environmental stresses and feeding insects play major roles in the fruiting behavior of cotton. Unfortunately, quantifications of these effects for inclusion into a simulation model is difficult. Using feedback, wherein fruit numbers recorded in a field are used as model input to correct within-season simulation, is one way to overcome this dilemma.[27,33]

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TABLE 1
Cultural Data for Cotton Grown near College Station, TX1/ in 1974 and Near Caldwell, TX2/ in 1985

	College Station 1974	Caldwell 1985
Planting date	28 April (d 118)	11 April (d 101)
Plant population (plants ha^{-1})	150,000	150,000
Row spacing (cm)	100	100
Cultivar	Stoneville 213	Deltapine 41
Assumed average boll size (g seed-cotton)	4.5	4.5

1/ Data from Keener.[34]
2/ Unpublished data.[36]

When the feedback option is used in COTTAM, numbers of squares and bolls are determined for each day by linear interpolation between feedback observation dates. Daily growth rates in square numbers are assumed equivalent to the growth in SITE using Equation 4. Growing and open boll numbers are determined from phenological aging. If the number of bolls obtained from feedback observations are fewer than those simulated, the difference is shed, beginning with the youngest bolls. If the simulated boll numbers are fewer, one half of the difference is added. If the number of squares determined from the feedback observations is less than that simulated, the difference is shed, as with the bolls. However, if the number of squares determined from feedback exceeds the number simulated, the growth in squares determined from feedback is assumed to represent the actual daily growth in fruiting sites and, hence, squares. After the last date of input feedback observations, Equations 4, 5, and (represented by) 7 are used to simulate fruiting dynamics without further restrictions.

IV. MODEL VERIFICATION

Verification of the COTTAM model is illustrated using two cotton data sets collected in central Texas. In the first, insect feeding apparently had little influence on the timing of yield development. In the second, insect feeding significantly delayed yield development. Both crops were irrigated and were assumed to be well watered (irrigation was simulated when plant available water in the soil profile declined below 50% of capacity).

The first data set was collected in 1974 by Keener[34] (these data are partially described by Curry et al.[35]). Cultural data are summarized in Table 1. For this cotton crop, fewer than 10% of the fruiting sites had shed squares at first flower appearance, indicating insect feeding was minimal. For the simulation, square and boll shedding due to insects was assumed to be negligible.

Simulated square and boll (including flowers) numbers show general agreement with those counted weekly (Figure 2), indicating the validity of the model. Simulated square numbers exceed those observed after d 175, and the 14.0 bolls $plant^{-1}$ on d 196 is greater than the 12.2 bolls $plant^{-1}$ observed. These differences are attributed to the assumption of no insect or water deficit effects on growth for this simulation (symptoms of mild water stress were reported during the season, see Keener[34]). The final open boll number simulated, 5.9 $plant^{-1}$, compares favorably with the 5.3 open bolls $plant^{-1}$ observed. The simulated lint yield was 1267 kg ha^{-1} and that measured was 1177 kg ha^{-1} (Table 2). Also, the appearance dates of first square, first boll (flower) and first open boll appear close to those observed showing the approximate square and boll periods. The date on which 50% of the final harvested bolls were opened can be used as an index of yield timing and the simulated date of d 222 is in close agreement with the d 225

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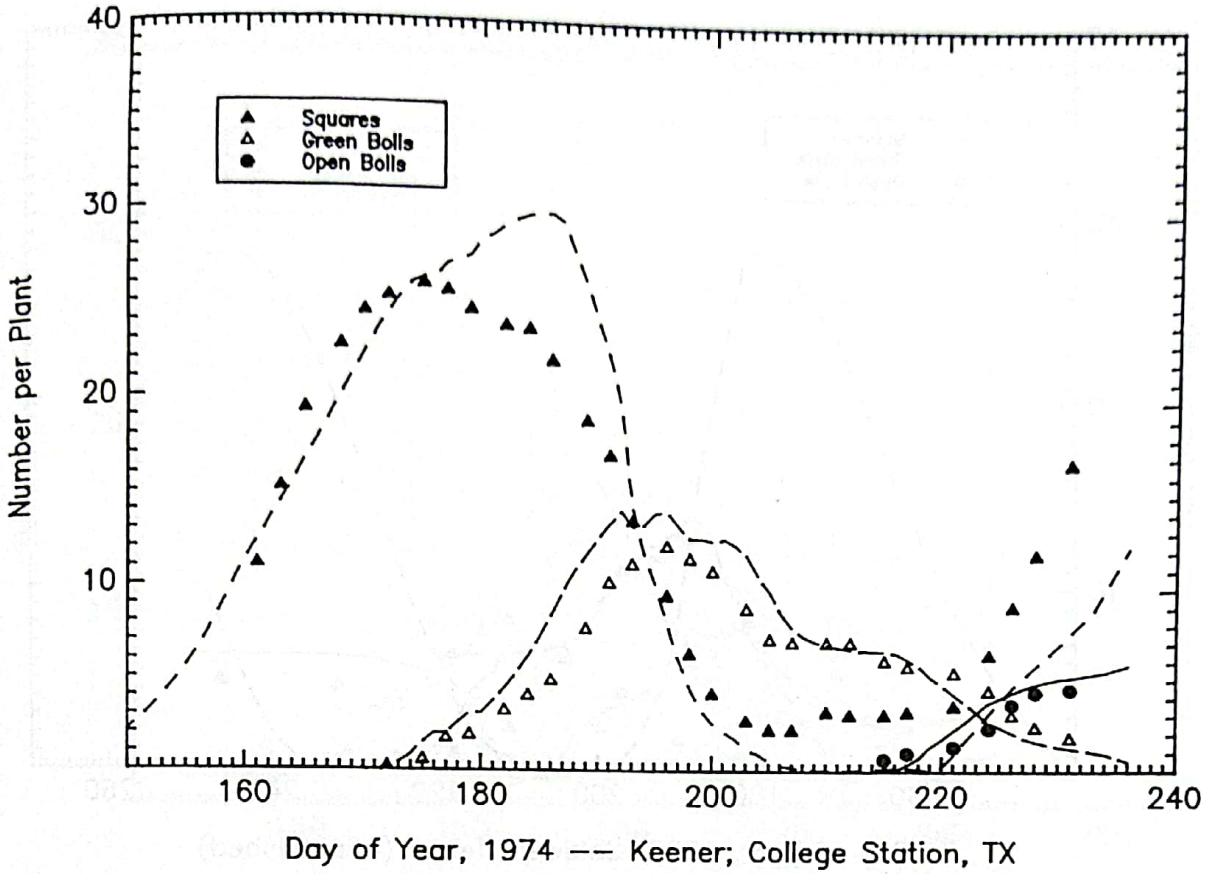

FIGURE 2. Comparison of measured (points) and simulated squares (short-dashed lines), flowers and green bolls (long-dashed lines), and open bolls for cotton grown near College Station, TX, 1974. (Data are from Keener.[34])

TABLE 2
Comparison of Measured and Simulated Yield Parameters from the Cotton Model COTTAM

	Measured			Simulated		
	Lint yield (kg ha^{-1})	Open bolls (plant^{-1})	50% Open bolls (day)	Lint yield (kg ha^{-1})	Open bolls (plant^{-1})	50% Open bolls (day)
1974	1177.0	5.3	225	1267.0	5.9	222
1987						
No. feedback	1375.0	4.7	238	1449.0	6.2	217
With feedback	"	"	"	1466.0	6.2	233

observed (interpolated).

The second verification data set was collected from a cotton variety, Deltapine 41, grown commercially in 1987.[33] Cultural data are summarized in Table 1. In 1987, however, 202 mm of rainfall was recorded during the period between d 145 and d 165, limiting pest management. As a result, many of the early squares were lost due to insect feeding. For example, the first squares were observed on d 142 but averaged only 1.0 plant^{-1} by d 155.

The simulation results shown in Figure 3 show that, although first square appearance was predicted with reasonable accuracy, peak square and boll numbers were simulated much earlier than observed. For example, the simulated date on which 50% of harvested bolls were opened was d 218, while the actual date was approximately d 238.

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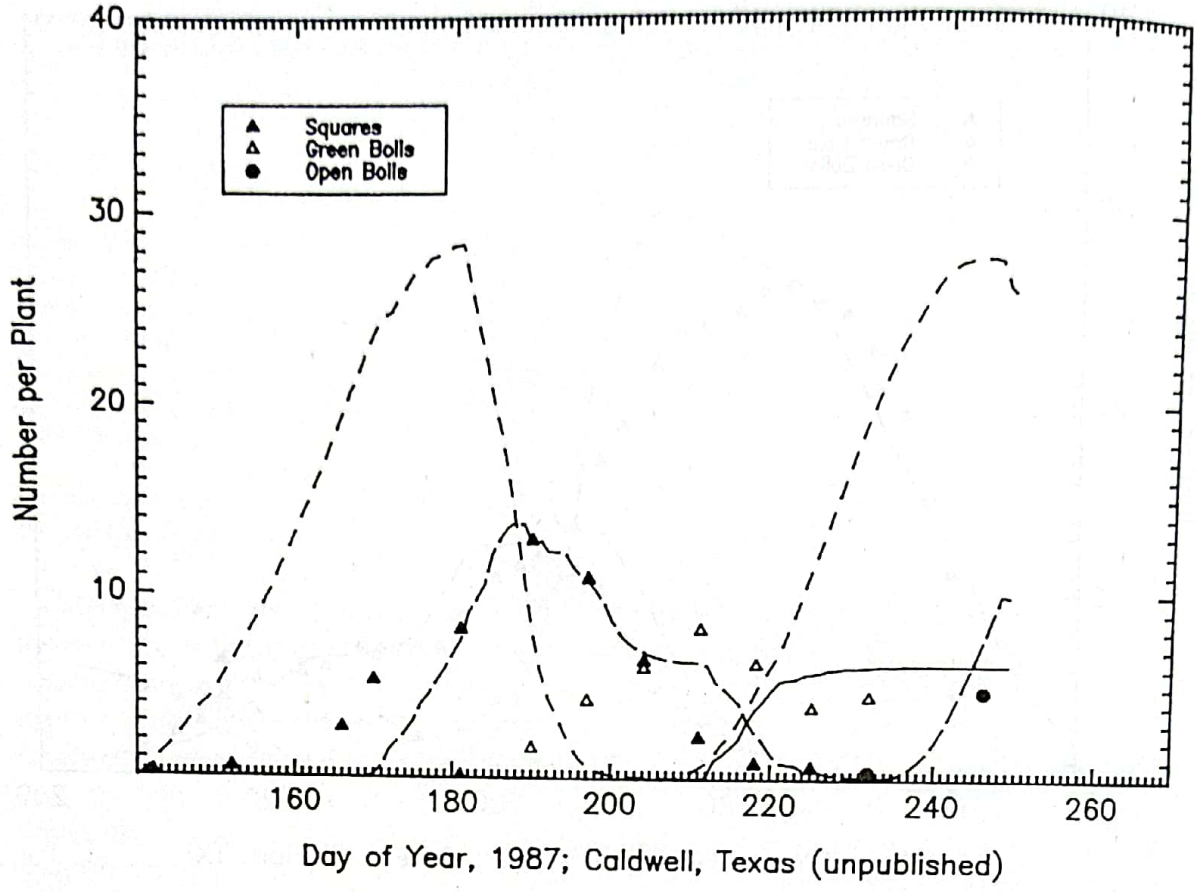

FIGURE 3. Comparison of measured (points) and simulated squares (short-dashed lines), flowers and green bolls (long-dashed lines), and open bolls for cotton grown near Caldwell, TX, 1985 (unpublished data[36]).

It is apparent from these data sets that the timing of yield development in cotton depends on the development rate of square and boll numbers as well as on the development rates of individual fruit. The feedback option described earlier is needed for the 1987 data set to account for the observed rate of development of square and boll numbers. Simulated square and boll numbers using those counted through d 181 are shown in Figure 4. Feedback forced the model to simulate square numbers observed through d 176. This adjustment moved the simulated date for 50% open bolls from d 217 (Figure 3) to d 233. Because feedback resulted in a better estimate of early season square shed and therefore, square numbers, the timing of peak boll numbers was also better represented.

In this case, including square and boll numbers as feedback input had little effect on simulated yields. Simulated open boll numbers, 6.2 plant^{-1}, were larger that the 4.7 open bolls plant^{-1} simulated (Table 2). Again, some of this difference is attributed to the assumption of no stress after the last date of feedback. However, simulated lint yields of 1466 kg ha^{-1} compare favorably with the 1375 kg ha^{-1} measured and the greater simulated open boll numbers may be compensation for the assumed boll size of 4.5 g seed-cotton boll^{-1} (Table 2), which may have been too small.

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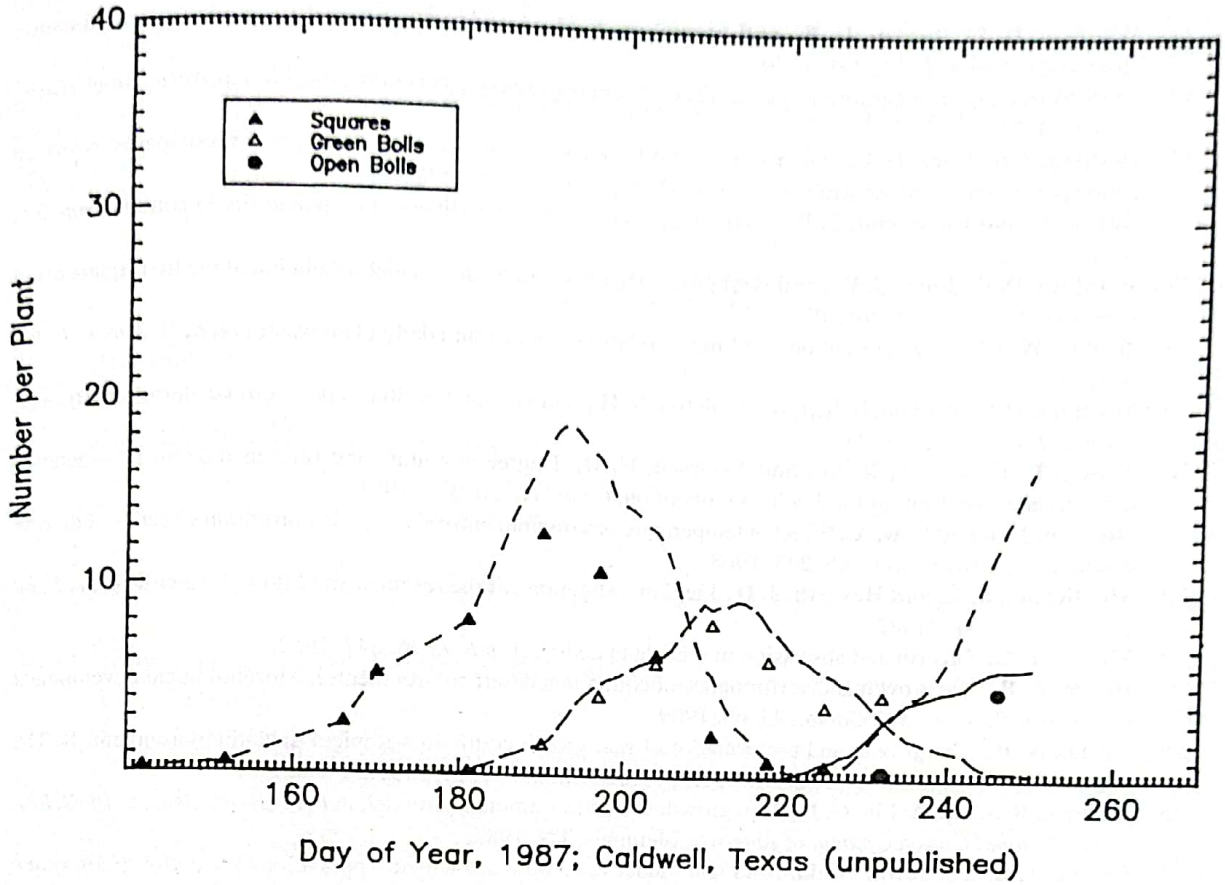

FIGURE 4. Comparison of measured (points) and simulated squares (short-dashed lines), flowers and green bolls (long-dashed lines), and open bolls for cotton grown near Caldwell, TX, 1985 (unpublished data[36]). Square and boll numbers were used as feedback input through d 181.

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Chapter 16

A MODEL FOR THE PHENOLOGY OF RICE

Evangelyn C. Alocilja and Joe T. Ritchie

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I. INTRODUCTION

This chapter contribution will describe the phenology component of the Crop Estimation through Resource and Environment Synthesis (CERES)-Rice simulation model for upland conditions. A lowland version, which takes into account the transplanting shock, is in the coding process.

Designed for the tropical and subtropical agroclimatic environments, CERES-Rice primarily predicts:

1. Phenological development or duration of growth stages as influenced by plant genetics, weather, and soil factors
2. Biomass production and partitioning
3. Effects of soil-water deficit and nitrogen deficiency on photosynthesis and photosynthate partitioning in the plant system

Programmed in FORTRAN 77, CERES-Rice is set up to run interactively in any IBM-compatible microcomputer with at least 256 K bytes of random access memory (RAM). In an IBM-compatible microcomputer with 640 K bytes RAM, simulation time of one cropping season takes about 25 to 40 s.

II. RICE GROWTH AND DEVELOPMENT

The growth cycle of rice (*Oryza sativa* L.) takes 3 to 6 months, depending primarily on temperature and genetic characteristics with regard to photoperiod sensitivity and thermosensitivity.[1,2] Because of weather factors, especially temperature and daylength, and genetic interactions, growth duration is highly site and season specific.

During the growth cycle, rice completes three major phenological stages: vegetative, reproductive, and ripening. The phenological events characterizing the vegetative stage are germination, emergence, juvenile growth, and panicle initiation (PI). The phenological events characterizing the reproductive and ripening stages are heading, grain filling, and physiological maturity.

The vegetative stage is characterized by root growth, active tillering, leaf initiation, leaf emergence, and increase in leaf area.[2]

Duration of the vegetative stage varies among cultivars and largely determines total growth duration.[2,3] The duration has minimum and maximum limits.[3] The minimum is relatively constant for a cultivar and is called the basic vegetative phase. The period between minimum and maximum limits is the photoperiod sensitive phase. Duration of the photoperiod sensitive phase depends on photoperiod and cultivar sensitivity to photoperiod. Photoperiod is a function of latitude (LAT) and day of the year (DOY).

The reproductive and ripening stages are characterized by root growth, stem elongation, increase in plant height, panicle development, panicle emergence, decline in tiller formation, grain growth, and leaf senescence. Duration of these two stages varies only slightly among cultivars.

III. MODELING RICE PRODUCTION SYSTEM

In describing the rice production system with a digital computer, the following discrete-time state-space equations are used:

$$\bar{x}(kT+T) = \bar{g}[\bar{x}(kt),\ \bar{u}(kT),\ \bar{e}(kT),\ kT]$$
$$\bar{y}(kT) = \bar{h}[\bar{x}(kt),\ \bar{u}(kT),\ \bar{e}(kT),\ kT]$$

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where k = discrete time, positive integer values exclusively; T = sampling interval; g and h = nonlinear vector-valued functions; y(kT) = output vector at discrete time k; u(kT) = controllable input vector at discrete time k; e(kT) = exogenous input vector at discrete time k; and x(kT) = state vector at discrete time k.

The sampling interval T is 1 d, that is, variable values are sequences of numbers spaced at 24-h intervals. For T equals 1, the state-space equations simplify to the following:

$$\bar{x}(k+1) = \bar{g}[\bar{x}(k),\ \bar{u}(k),\ \bar{e}(k),\ k]$$

$$\bar{y}(k) = \bar{h}[\bar{x}(k),\ \bar{u}(k),\ \bar{e}(k),\ k]$$

Vector components of u(k) are cultivar, sowing date, number of plants m^{-2}, depth of sowing (cm), day, amount (kg N ha^{-1}), depth (cm) and type of nitrogen (N) fertilizer applied, day, and amount of irrigation (mm).

Vector components of e(k) are solar radiation (MJ m^{-2}), maximum and minimum air temperatures (°C), and rainfall (mm day^{-1}) at time k.

Vector y(k) has two components: grain yield (t ha^{-1}) and plant straw (g m^{-2}).

Soil properties and initial conditions define the system parameters.

IV. FACTORS AFFECTING RICE PHENOLOGY

In the model, there are four genetic coefficients associated with phenology: P1 (thermal time required from emergence to end of juvenile stage), P2R (rate of photo-induction, in degree days per hour), P2O (optimum photoperiod, in hours), and P5 (thermal time required for grain filling and to complete physiological maturity).

Phenological events and stages in the model are numbered one through nine, with the above-ground stages numbered one through five. This numerical sequencing is used to partition carbohydrate, which varies according to phenological stage. The events and stages are defined as follows: sowing (ISTAGE 7), germination stage (ISTAGE 8), emergence stage (ISTAGE 9), juvenile stage (ISTAGE 1), PI stage (ISTAGE 2), heading stage (ISTAGE 3), pre-grain filling stage (ISTAGE 4), grain filling stage (ISTAGE 5), and physiological maturity (ISTAGE 6).

The duration of each phenological stage makes use of the concept of thermal time or degree days at time k (DTT(k)). DTT(k) is a function of minimum (TEMPMN(k)) and maximum (TEMPMX(k)) air temperatures and temperature threshold (TBASE). From a series of phytotron studies,[4] the threshold temperature of rice is estimated to be 8°C. When TEMPMN(k) is greater than TBASE and TEMPMX(k) is less than 33°C, DTT(k) is the difference between daily mean temperature (TEMPM(k)) and TBASE. TEMPM(k) is calculated as the average between TEMPMX(k) and TEMPMN(k). That is

$$\text{TEMPM}(k) = \frac{1}{2}\left(\text{TEMPMX}(k) + \text{TEMPMN}(k)\right)$$

$$\text{DTT}(k) = \text{TEMPM}(k) - \text{TBASE}$$

Otherwise, DTT(k) is estimated by dividing a 24-h day into 8 3-h sections, calculating a temperature correction factor for each section (TMFAC(k)), interpolating the air temperature for that 3-hour section (TTMP(k)), and then calculating the appropriate thermal time at time k. That is

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$$TMFAC(k)_i = 0.931 + 0.114i - 0.0703i^2 + 0.0053i^3, \quad i = 1, \ldots, 8$$

$$TTMP(k)_i = TEMPMN(k) + TMFAC(k)_i\left(TEMPMX(k) - TEMPMN(k)\right), \quad i = 1, \ldots, 8$$

$$DTT(k) = \begin{cases} \frac{1}{8}\sum_{i=1}^{8}\left(TTMP(k)_i - TBASE\right), & TBASE < TTMP(k)_i \\ \frac{(33 - TBASE)}{8}\sum_{i=1}^{8}\left[1 - \frac{1}{9}\left(TTMP(k)_i - 33\right)\right], & 33°C < TTMP(k)_i < 42°C \\ 0, & \text{otherwise} \end{cases}$$

The relationship between i and $TMFAC(k)_i$ is shown in Figure 1.

V. MODELING PHENOLOGICAL EVENTS AND STAGES

A. SOWING

Sowing occurs when seeds are sown in the ground. Discrete time k is set to 0, i.e., k = 0, and will be incremented by 1 every simulation step hereafter.

B. GERMINATION STAGE

The germination stage covers the period from sowing until germination. In the model, germination will occur if all of the following four conditions are satisfied:

1. Either, (a) there is enough moisture in the soil-seed layer, that is,

$$SW(k)_{\lambda 0} > LL_{\lambda 0}$$

where SW(k) is the soil water content of the seed layer λ0 at time k and LL is the lower limit of plant extractable soil water of that layer, or (b) the extractable soil water (SWSD(k)) is 0.02 or greater. This extractable water is calculated proportionately between SW(k) and LL of the seed layer λ0 and the layer below it, λ0+1, that is,

$$SWSD(k) = 0.65\left[SW(k)_{\lambda 0} - LL_{\lambda 0}\right] + 0.35\left[SW(k)_{\lambda 0+1} - LL_{\lambda 0+1}\right] \geq 0.02$$

2. Mean air temperature at time k is between 15 and 42°C, that is,

$$15°C \leq TEMPM(k) \leq 42°C$$

Livingston and Haasis[5] showed that complete germination of healthy rice seeds occurred between 15 and 37°C. At the incubation temperature of 42°C, only about 8% germinated in 10 d, and no germination was observed in a period of 6 d at 45°C.

3. Accumulated thermal time after sowing is 45 or more. This condition was derived by applying the concept of thermal time to the data of Livingston and Haasis.
4. Duration of the seeds in the ground is no more than 40 d. If germination does not occur by 40 d after sowing, crop failure is assumed and the simulation ends.

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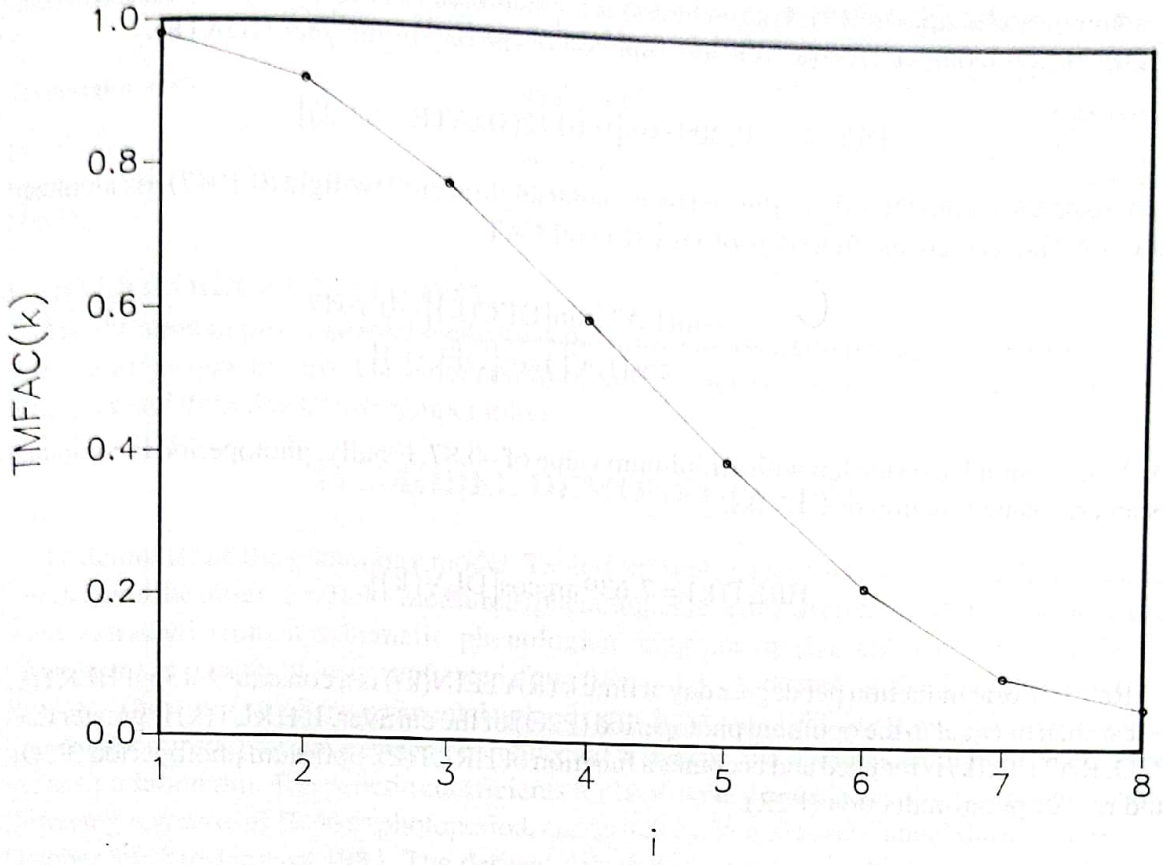

FIGURE 1. The relationship between i and $TMFAC(k)_i$.

C. EMERGENCE STAGE

Emergence stage is the period from germination to emergence. Emergence occurs when the tip of a seedling emerges from the soil surface and autotrophic growth begins.[2] The duration, in degree days, is P9, which is a linear function of the sowing depth (SDEPTH) with a slope of 7 degree days per cm depth.

$$P9 = 7[SDEPTH]$$

D. JUVENILE STAGE

The juvenile stage covers the period from seedling emergence to the end of the basic vegetative phase. The thermal time required to complete the juvenile stage is the genetic coefficient P1, which is determined for a cultivar by flowering studies in either a phytotron or in the field.

E. PANICLE INITIATION STAGE

The PI stage in the model covers the period from the end of the basic vegetative phase to PI. Rice is a short-day crop, initiating panicle primordia in response to short photoperiods.[2] The duration of the PI stage varies with cultivar photoperiod sensitivity and photoperiod. The daylength at which the duration from sowing to flowering is at a minimum is called the optimum photoperiod.[2,6] The critical photoperiod is the longest photoperiod at which the cultivar will flower.[2,6] Photoperiod sensitivity is a genetic trait, that is, the critical and optimum photoperiods differ among cultivars. The growth duration of a cultivar that is less sensitive to photoperiod does not fluctuate as much as a highly sensitive cultivar under different daylength conditions.[1]

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Photoperiod at time k (HRLT(k), in hours) is a function of LAT and solar declination at time k (DEC(k), in radians). DEC(k) is a sine function of the day of the year (JDATE).

$$\mathrm{DEC(k)} = 0.4093 \sin\left[0.0172(\mathrm{JDATE} - 82.2)\right]$$

Daylength variation (DLV(k)), adjusted by the solar angle at civil twilight (0.1047), is calculated from the sine and cosine functions of DEC(k) and LAT.

$$\mathrm{DLV(k)} = \frac{-\sin(\mathrm{LAT})\sin\left[\mathrm{DEC(k)}\right] - 0.1047}{\cos(\mathrm{LAT})\cos\left[\mathrm{DEC(k)}\right]}$$

DLV(k) is bounded on the left with a minimum value of –0.87. Finally, photoperiod is computed as an arccosine function of DLV(k).

$$\mathrm{HRLT(k)} = 7.639 \arccos\left[\mathrm{DLV(k)}\right]$$

Rate of floral induction per degree day at time k (RATEIN(k)) is a constant 1/136 if HLRT(k) is less than or equal to the optimum photoperiod (P2O) of the cultivar. If HRLT(k) is greater than P2O, RATEIN(k) is reduced and becomes a function of HRLT(k), optimum photoperiod (P2O), and rate of photo-induction (P2R).

$$\mathrm{RATEIN(k)} = \frac{1}{136 + \left(\mathrm{P2R}\left[\mathrm{HRLT(k)} - \mathrm{P20}\right]\right)}$$

As mentioned earlier, P2O and P2R are genetic coefficients in the model. The PI stage is completed when the sum of the product of RATEIN(k) and DTT(k) from the beginning of this stage (k_2) until time k_p is 1.0, where k_p is the day of PI. That is

$$\sum_{k=k_2}^{k_p} \mathrm{RATEIN(k)}\left[\mathrm{DTT(k)}\right] = 1.0$$

F. HEADING STAGE

The heading stage is from the end of the PI stage to the time when 50% of the panicles have fully exserted. The duration of the heading stage is P3. It is equivalent to 450 degree days plus 0.15 of the accumulated degree days from the beginning of the juvenile stage (k_1) until PI (k_p).

$$\mathrm{P3} = 450 + 0.15 \sum_{k=k_1}^{k_p} \mathrm{DTT(k)}$$

G. PRE-GRAIN FILLING STAGE

The pre-grain filling stage is from the time when 50% of the panicles have exserted to the beginning of grain filling. The duration is 170 degree days.

H. GRAIN FILLING STAGE

The grain filling stage covers the period of grain filling. The duration, in degree days, is 0.95 of the genetic coefficient P5.

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TABLE 1
Comparison between Predicted and Observed Dates of Phenological Events for Cultivar IR36 (Sowing Date: 9 January 1980)

Phenological event	Predicted	Observed
PI	29 February	28 February
Heading	31 March	30 March
Maturity	28 April	28 April

I. PHYSIOLOGICAL MATURITY

The duration of physiological maturity is the time required to complete P5 or when DTT(k) is less than or equal to zero. The latter condition stops simulation even with insufficient thermal time accumulation due to low temperatures.

IV. MODEL DEMONSTRATION

To demonstrate the phenology model, Table 1 presents a comparison between the predicted (model) and the observed (field-measured) phenological events for cultivar IR36. Observed data were extracted from a schematic phenological diagram of five cultivars by Chinchest.[7] Chinchest's experiment was replicated four times and conducted at the International Rice Research Institute (IRRI) experimental upland farm during the 1980 dry season. Actual weather data for the duration of the experiment, collected at the site and obtained from IRRI, were used in the simulation run. The genetic coefficients for IR36 were derived from the experiment on the flowering response of IR36 to photoperiod, conducted by Vergara and Chang[8] during the period October 1982 to January 1983. The derived values of the genetic coefficients are as follows:

P1 is 590 degree days; P2R, 124 degree days/hour of photoperiod; and P2O, 11.7 h. The genetic coefficient P5 is estimated to be 550 degree days. Predicted dates of floral initiation (FI) and heading were a day later while predicted date of maturity was the same compared to the observed dates.

Table 2 presents a comparison between the predicted (P) and the observed (O) phenological occurrences, in days after sowing (DAS), for three upland rice cultivars: IR43, UPLRi5, and UPLRi7. Field-measured data are from a series of experiments on drought tolerance conducted during 1983 and 1984 at IRRI, Los Banos, Philippines.[9] Actual weather data collected at the site were used in the simulations. Sowing dates were based on actual data. In the absence of flowering response studies on these cultivars, the genetic coefficients were estimated from one of the experiments, other than those presented in Table 2. That means that in this case, the phenology model was "calibrated" for the location. The three phenological events compared are seedling emergence, heading, and physiological maturity. The comparison showed that from an average of 6 experiments, the predicted date of emergence was 1 d less than the observed date for the three cultivars. However, the predicted date of heading was 1 d earlier for IR43, 2 d later for UPLRi5, and 4 d earlier for UPLRi7, compared with the observed data. The predicted occurrence for physiological maturity was only a day earlier than the observed for IR43 and UPLRi5, while about the same, on the average, for UPLRi7.

A chi-square analysis was done on the observed and predicted dates. The null hypothesis is that the field-measured and model-generated data for emergence, heading, and maturity are not statistically different. The results, as tabulated in Table 2, show that all the calculated χ^2 are less than the critical χ^2 value at 0.05 level of significance. The null hypothesis is accepted, which means that the predicted dates are not different from the observed dates.

Table 3 presents the morphological characteristics of IR36, IR43, and UPLRi5, as provided by IRRI. The three cultivars differ with respect to morphology. For example, the seedling of UPLRi5 is taller and the leaves are longer and wider compared to IR36 and IR43. However,

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TABLE 2
Comparison between Predicted and Observed Phenological Occurrence of Three Rice Cultivars Days after Sowing (DAS)

Cultivar name	Sowing date (1983)	Emergence		Heading		Maturity	
		P	O	P	O	P	O
IR43	May 26	4	8	99	97	128	125
	June 30	4	6	96	99	127	134
	July 8	4	4	97	99	128	127
	August 4	4	4	95	100	127	123
	August 28	4	4	94	100	127	127
	November 10	4	6	98	93	129	134
	(Average)	4	5	97	98	127	128
	Computed χ^{2*}	6.0000		1.0766		0.7837	
UPLRi5	June 20	4	4	98	95	121	119
	June 30	4	6	98	92	120	116
	July 8	4	4	97	95	120	120
	August 4	4	4	94	100	118	123
	August 28	4	4	93	93	117	116
	November 10	4	6	96	91	119	125
	(Average)	4	5	96	94	119	120
	Computed χ^2	2.0000		1.1438		0.6893	
UPLRi7	May 26	4	8	92	91	119	116
	June 20	4	4	89	88	117	112
	June 30	4	6	88	91	116	116
	July 8	4	4	88	89	117	119
	August 4	4	4	86	99	115	123
	August 28	4	4	84	93	115	116
	(Average)	4	5	88	92	117	117
	Computed χ^2	5.0000		3.0651		0.8887	

* $\chi^2 = E \dfrac{(f_o - f_p)^2}{f_p}$ with degrees of freedom = 5

where: f_o = observed date; f_p = predicted date. The critical χ^2 value at a = 0.05 is 11.070.

while the culms are longer for UPLRi5, the number is less compared with IR36 and IR43. The flag leaf angle orientation of IR36 is descending, that of IR43 is intermediate, and that of UPLRi5 is horizontal. IR36 has the shortest growth duration (105 d, under Los Banos condition), while UPLRi5 has the longest maturity period (124 d). IR43 has a growth duration of 111 d.

V. CONCLUDING REMARKS

An initial demonstration of the phenology of CERES-Rice (upland version) shows that the predicted dates of emergence, PI, heading, and maturity are not different from the observed dates. This implies that the phenology model can be used to predict the occurrence of phenological events of rice crops. Studies on the flowering response to photoperiod need to be conducted for IR43, UPLRi5, and UPLRi7 in order to verify the genetic coefficients. More validation tests are still required to establish its predictive capabilities in other parts of the rice-growing areas.

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TABLE 3
Morphological Characteristics of IR36, IR43, and UPLRi5

Character	IR36	IR43	UPLRi5
Seedling height (cm)	28	26	35
Leaf length (cm)	39	40	54
Leaf width (cm)	0.9	1.1	1.2
Flag leaf angle	Descending	Intermediate	Horizontal
Culm length (cm)	58	72	105
Culm no.	18	17	16
Panicle length (cm)	21	26	26
Spikelet sterility	75-90%	75-90%	75-90%
100-grain wt (g)	2.3	2.7	2.2
Grain length (mm)	8.8	9.2	9.3
Grain width (mm)	2.7	2.9	2.8
Leaf senescence	late	late	late
Maturity*	105	111	124

* Duration from seedling to full heading plus 30 d.

There are also some fundamental issues that need to be resolved, pending more evidence from experimental data. For example, does drought or nitrogen deficiency affect the phenological events? If so, what is the effect—hastening the occurrence of the event or delaying it? Similarly, what is the effect of too much nitrogen? Because of these and other issues, the phenology model would likely be updated whenever research information is available.

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Chapter 17

WEED PHENOLOGY

D. M. Alm, M. E. McGiffen, Jr., and J. D. Hesketh

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I. INTRODUCTION

Weed scientists are concerned with the economic control or elimination of weeds. Weeds, from a productionist's perspective, are plants out of place. Many scientists are also concerned with the effect of weed control methods on water quality and other components of the ecosystem. There are many aspects to this overall problem; here, we are particularly interested in predicting the phenological behavior and related responses of weeds competing with crops. Such predictions and related concepts can be used for making management decisions or for studying crop-weed system behavior. The objective of the latter is to find a weak link in the system that can be manipulated for better weed control.

Models have been developed for a few major crops, based upon extensive research on cultivar behavior. Building models for cultivars or races of other species not as well studied presents problems, particularly when interspecific competition is a factor. Gutschick,[1] in an analysis of how plants acclimate or adapt to environmental-physiological stresses, emphasized the importance of the phenotype as controlled by phenology, morphology and physiology (Table 1). He discussed "strategies" for coping with drought, nutrient deficiency (carbohydrate, minerals), and cold/heat stress with related recent literature. How two kinds of plants compete depends upon differences in their "strategies" for utilizing available resources. Salisbury and Marinos[2] listed the same three factors, but broke the "physiology" term down into (1) the reduction of growth and metabolic activities and (2) the conservation of resources (metabolic energy, water). They emphasized morphology and developmental physiology, particularly the role of plant growth substances. Both reviews emphasized the importance of phenology in plant adaptation or acclimation mechanisms.

Radosevich and Holt[3] noted three key factors in crop-weed competitive systems: (1) timing of germination or sprouting of buds on underground storage organs or overwintering shoots (apical or basal), (2) growth rate, and (3) the spatial arrangement of the plants involved. A plant that emerges early will gain an initial competitive edge over late-emerging plants. The first plants up, however, are not necessarily the most competitive. If a late-emerging weed has a faster growth rate than the crop or other weeds, then it may surpass the other species and become the dominant one in its area of influence[4] (the assumed circular area within which a weed affects the crop and other plants and vice versa).

Gutterman[5] and Kigel and Koller[6] emphasized the importance of the timing, growth rate and spatial characteristics of sexual and asexual reproduction as key factors in crop-weed competitive systems. Distribution of seeds or asexual reproductive units by cultivation can enhance the competitiveness of most weeds. We will concern ourselves here with describing the phenological aspects of predicting competitive behavior.

There are many process levels within an agricultural plant community, from the organelle to a large geographic unit, that a weed-crop competition model might reflect. The attention a particular level should receive depends upon how the component processes at that level control the behavior to be predicted, how well those processes can be quantified, and the modeling of objectives.

One obvious goal of a weed-crop model might be to predict yield reductions due to competition for resources. Zimdahl[7] cited nearly 600 publications involving yield reductions due to weeds. Most of these involved yield and economic losses at predetermined, often arbitrary weed population densities. There are, of course, many possible weed community age- and size-class structures within an area much smaller than a farmer's field. In addition, cultural practices can continually modify the community structure, e.g., cultivation somewhat limits weeds to the cohorts emerging in the vicinity of the row of crop plants. Sampling a field for weed density and spatial distribution therefore presents problems that must be considered at the early stages of development of a phenological model; the input and output structure of a phenological model should be logically and structurally compatible with a model of community behavior.

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TABLE 1
Physiological, Morphological and Phenological Traits Interacting with Environment to Create Strategies for Adapting or Acclimating to Stress

Phenotypic traits:

Volumes, weights, composition (including water), energy status (temperature), and spatial coordinates of various organs (phytomers, roots, reproductive and/or storage organs) at various developmental or growth stages, concentration or chemical potential gradients, flux resistances

Physiological processes:

Photosynthesis: C_4, C_3, C_3-CAM, C_3-CO_2 membrane pump

Transport: phloem loading or unloading, membrane transport, osmotic pump, water movement

Storage: starch, fructosans, sugars

Respiration: capital (growth and development), operational, maintenance, heat production

Transpiration: evaporative cooling

Energy balance: convective, advective, radiative heat exchange, evaporative cooling

Mineral nutrition: rhizobial N-fixation, root or leaf N-reduction, redistribution or scavenging, membrane transport

Development: changes in form, structure, state of complexity, cell division, differentiation, morphogenesis, plant growth regulator physiology, apical dominance, photoperiodism, sexual and asexual reproduction, dormancy, vernalization, senescence, abscission

Growth: irreversible quantitative increases in volume or weight, leaf expansion, internode and root extension, growth equations, phototropism, gravitropism, anatomical responses.

Morphological options:

Roots: (10 forms, standard college dictionary), fibrous, tap or modified storage, prop, aerial, mycorrhizal or rhizobial associations, adventitious root and shoot buds

Stems: (20 forms, with numerous subclasses to give over 100 forms, attributed to C. Drude in the early 1900s,[148] numerous other classification systems[148,149]), woody conifers and dicots, herbaceous dicots and monocots; modified storage; phyllotaxy; determinate and indeterminate main or lateral; internode length and angle; apical, lateral, adventitious, intercalary, cambial, and cork meristems

Leaves: size and shape (52 forms for broad-leafed species, standard college dictionary), orientation, petiole length and angle, sheath size and shape, modified storage (bulb), stomatal size, shape and distribution, hairs

Storage organs: fruit, seed, modified root and shoot organs.

Vegetative reproductive organs: prostrate lateral branches with nodal roots — modified as stolons, rhizomes, and tubers; corms, bulbs; adventitious buds on leaves, stems, fleshy tap or horizontal lateral roots.

Relevant tissues, cells or organelles: see anatomy books.

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TABLE 1 (continued)
Physiological, Morphological and Phenological Traits Interacting with Environment to Create Strategies for Adapting or Acclimating to Stress

Phenology:	Carefully defined morphological stages of growth, development or maturity based upon size or shape or duration as thermal or real time (note — phenology often quantifies growth or developmental rates, or is a measure of these process rates).
	Thermal time units based upon responses of potential (adequate supply of nutrients) growth and/or development to temperature, base temperature, optimum temperature, limiting upper temperature
	Photothermal time units based upon photoperiod and thermal units.
Environment:	Air-soil temperatures, water content, gas mix, nutrients, irradiance levels, spatial gradients and variation, short and long-term dynamics of soil morphology (macropore dynamics)
Adaptive or acclimation mechanisms:	Escape, avoidance, tolerance, or endurance to light, flooding, salt, drought, frost-freeze, heat, mineral stresses,[150] biological pests[151-153] and their spatial dynamics[154]

II. A MODERN DEFINITION OF PHENOLOGY

Phenology is the study of periodic biotic events, which traditionally meant events that occurred once in a growing season. In the past, such studies were for whole organisms; one can also study periodic events that occur much more frequently at the organ, tissue, or cellular levels (Table 1). Phenology represents a way of measuring rates of growth and developmental processes (and is affected by the phenotype while measurements are being made), physiological processes controlling growth and development, and the environment.

For a history of the concept and some definitions of metamer behavior, or "plant metamerism", see White[8] or Watson and Casper.[9] A plant phytomer,[8] synonymous with metamer, is a morphological unit made up of a leaf, internode, node and axillary and adventitious buds. The components of a phytomer can become greatly modified, as in a floral or vegetative-storage organ. A phytomer, or a collection of modified phytomers making up a larger organ, has become a useful unit for phenological analyses, with periods between similar events during the life cycle of phytomers defined by their position on the plant. Detailed phenological stages of flowers have been carefully defined and used for some time to describe growth stages in flowering research. Phenology is essentially the study of the dynamics of development, with emphasis on the inherent schedule of events, rather than interevent processes.

The progress of a succession of events may not always be smooth. Mayer,[10] in discussing dynamic morphology in animals, notes that experimental inhibition of mitotic activity may be followed by a wave of increased activity which rapidly stabilizes to a constant rate. An analogous situation in plants is compensatory branching,[11] or an accelerated rate of leaf primordia initiation after floral induction.[12] Thus, growth and developmental aspects of phenology on a short-term basis may not always be the simple product of phenological rate and stress functions, and without careful analysis of the system, it may not always be clear whether environment has a direct or indirect affect on a phenological rate, as illustrated by the previous examples.

Weed and crop plants typically have a high degree of phenotypic plasticity[13] (variability in morphological appearance at the same stage of growth among plants with the same genetic makeup, as a result of their prior environmental history), which we hope to be able to predict. This suggests that environmental effects on phenology must be large and therefore easy to

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quantify, but difficult to predict within a small error limit. Logarithmic growth rates over time, or logarithmic responses to environmental factors such as temperature, result in large changes that are difficult to pinpoint with a small error. Early growth differences when plants are small may later directly result in large differences, which can be explained only if the earlier differences are properly noted. These early differences may be evident only when the relative dimensions of individual organs are compared.

Recent attempts[14-25] to quantify the weed-crop behavior as part of a crop production model have demonstrated the need for more phenological information, particularly that related to leaf area development and display in both crops and weeds. Waller[26] divided growth analysis research into (1) traditional methodology involving leaf area and dry weight measurements for shoots and roots, (2) yield component analysis, and (3) the demographic tracking of plant parts over time (in essence, organ phenology). Crop modeling has gone one step further to combine aspects of all three of these approaches with detailed measurements of gas exchange, nitrogen and water uptake coupled with those of organ appearance and maturation. The result is a synthesis of growth and development based upon a materials budget and supply-demand effects on further growth and development.

Temperature, available water, and nitrogen are the primary environmental factors considered in most crop models. Phenology interacts with the environmental physiology of plants; the timing of the appearance of organs is to some degree coupled with the developmental rates of organs that have already appeared and vice versa. In a synthesis, one needs a materials budget for phytomers at various stages of growth and development for plants growing under a range of environments leading to different levels of materials supply and demand. It is important to know the minimum and maximum limits of various materials to the growth of a phytomer at various defined phenological stages, especially for a storage or fruiting organ that will be harvested for yield. The behavior of the array of vegetative phytomers on a plant during fruit set or storage organ development, particularly in response to environmental stresses leading up to fruit or storage organ maturity, determine the yield components.

III. COMPETITION MODELS

The step from predicting how a cultivar of one species behaves to how several races or species interact or compete in a cropping or natural system is a major one. A main complicating factor is defining the spatial arrangement of the plants involved. Before discussing weed phenology, we need to give a summary of the status of the prediction of crop:weed competitive systems and explain how spatial factors are handled.

The ecological literature and, recently, the agricultural literature, presents many theoretically derived models of plant competition and experimental attempts to validate those models. Most of these models are spatially one-dimensional. We will describe some of these models and point out that the one-dimensional character and resultant lack of attention to development and form may lead to elegant equations, but lead away from important aspects of reality: species-specific competitive mechanisms. We hope to convince the reader that a mechanistic model of the effects of competition on phenology, and vice versa, necessarily involves the modeling of development and form at the phytomer level.

A. REGRESSION MODELS

Radosevich[27] defined three aspects of plant proximity: density, the fraction of each species in the population (proportion), and spatial arrangement. At typical crop densities, total biomass of the crop plus weeds is independent of density.[28] As total density of all species present increases, total resources available for growth are divided by more and more plants, resulting in decreased biomass or yield per plant.

The relationship between individual plant weight (W) and density (D) is given by the reciprocal yield law:[29]

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$$W^{-\alpha} = \beta + \gamma D \quad (1)$$

where β and γ are environmental and species dependent variables and represent the degree of nonlinearity in the relationship between W and D. α is often approximately one, giving

$$\frac{1}{W} = \alpha + \gamma D \quad (2)$$

where Δ is the reciprocal of the maximum weight of a plant grown alone, and ε is the slope of the relationship between W and D, and as such gives a measure of the intraspecific competition associated with increasing plant density.

Equation 2 can be expanded to include the effect of the proportion of different plant species present in mixed stands:[30]

$$\frac{1}{W_1} = \beta_1 + \gamma_{11}D_1 + \gamma_{12}D_2 + \gamma_{1i}D_i \quad (3)$$

where W_1 is the weight of individual plants of species 1, and D_1, D_2, and Di are the densities of species 1, 2 and i, and γ_{1i} (i = 1 through n) quantifies the effects of intraspecific competition on plant weights for species i.

The theoretical study of Fischer and Miles[31] on the effects of spatial arrangement on competition has been frequently cited, but research on spatial aspects of crop-weed competition has been scant. It is well known that weeds are seldom randomly distributed within production fields, but the effect of weed distribution on data analysis and interpretation is often ignored in such studies. The degree of clumping of pest populations within a crop profoundly affects the relationship between numbers of pests present and decrease in yield.[32] The models of Benjamin and Hardwick[33] and Sutherland and Benjamin[34] relating crop growth and yield to the spatial arrangement of plants and available (captured) resources may provide a base upon which to develop a model for predicting the spatial effects of crop and weed plants on crop losses.[35]

Radosevich[27,36] reviewed experimental methods for studying competition, which he broke down into three designs: (1) additive, (2) replacement and (3) sphere (area) of influence. In additive experiments, the density of one species (e.g., the crop) is held constant while the density of the second species (the weed) is varied. Additive experiments mimic agricultural situations in which a crop of predetermined density is infested by weeds. Both total plant density and the changes in proportions of the two species in the total plant population are compounded in the observed yield reduction. The effect of spatial pattern on competition cannot be determined, nor can inter- or intraspecific effects be separated.

Replacement experiments overcome the limitations of additive designs by holding total plant density constant, while the weed-to-crop proportion of the total population varies.[28] Spitters[37] and Radosevich,[27] based on the earlier work of de Wit,[38] examined the biomass yields of replacement series experiments by comparing a series of theoretical possibilities. The responses mimic those predicted by Raoult's law for the proportion and total amount of vapor in the atmosphere above a two-component solution. There are four basic responses: (1) no competition, (2) one species competing more effectively for resources than the other, (3) mutual antagonism, as when each species produces alleopathic chemicals that inhibit the other, and (4) a mutually beneficial effect of a species mix on total biomass production, such as when one species fixes nitrogen that the other can use and the other inhibits a disease that might be affecting the N-fixer. Models analogous to Raoult's law have been used to analyze pasture or hay production, where a mix of grasses and legumes or a mix of species adapted to cool and warm

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climates is maintained. The major problem with this approach is applying results to cropping situations in which the crop plant density is constant but the total plant density varies.

In the sphere-of-influence design,[4] weeds are established within crop rows and crop plants are sampled at varying distances from a weed plant or groups of plants. The plant densities within the row are converted to field densities, assuming no row-to-row or intraspecific weed effects. The sphere-of-influence design has distinct advantages in that it requires less space than replacement or additive designs. This method works best when crop plant-to-plant variability in the row is minimized, and the weed is a strong competitor, such as is the case with volunteer maize plants in a soybean stand.[39] The assumptions described here must be taken into account prior to conducting such an experiment, particularly with species that have not been tested before in such an experimental design.

B. SIMPLE DYNAMIC MODELS

Spitters and van den Bergh[24] simulated competition as the ability of a plant to exploit resources available for growth. Resources were denoted as "relative space" or RS_i, with i specifying the time period involved. Plant biomass per unit ground area, W, (one could substitute leaf area) was hyperbolically related to plant density D:

$$W = \frac{\eta D \theta}{(\eta D + 1)} \tag{4}$$

Double reciprocal plots of biomass vs. density (1/W vs. 1/D) at time t gives estimates of η. θ represents the yield as D approaches infinity and η yield as D approaches 0. The space occupied by one plant in the population is $\eta/(\eta D + 1)$. They obtained η values vs. time from a time series of plots of biomass vs. density, for both a weed and a crop. Both $\eta(t)$ functions were logarithmic during early growth.

Space immediately implies leaf area per plant. Alm and co-workers[15-17] measured leaf area development in crop and weeds, taking into account the time from planting to germination. One could easily set an upper boundary for leaf area per unit ground area for when to determine the fraction of area contributed by each species and then manipulate density, germination date, or the initial area and the relative leaf area expansion rate [for A = area, (1/A)(dA/dt) or R_A]. Such a model lacks the density effect on R_A that Spitters and van den Bergh[24] accounted for in their system.

The analysis of these models is educational, but many major weeds seem to defy the assumptions by performing well in the shade of the crop, seeking out holes in the crop canopy, and growing rapidly above the crop canopy through such holes. Row and cultivation effects also need to be taken into account, all of which brings us to the next level of model complexity.

C. COMPLEX DYNAMIC SYSTEMS MODELS

The reciprocal yield law (Equation 1) quantifies a competition effect as a depression in yield caused by the proximate factor density. Although numerous researchers have demonstrated the utility of this approach, the competitive process is clearly a complex one influenced by many interacting factors.[14] A systems modeling approach theoretically provides insight into complex processes by quantifying underlying mechanisms that lead to an observed response.

It is a small step from the Spitters-van den Bergh[24] model to a full-fledged systems model. They[24] expanded on the additive approach by attempting to quantify competition for "space" (Equation 4), space being associated with limiting resources such as light, water or nitrogen. Their space factor does not account for volume effects and is difficult to measure or define quantitatively.[40] Examples of volume or three-dimensional differences include (1) the ability of velvetleaf (*Abutilon theophrasti* medic.) to shoot up rapidly into full sunlight above a crop

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canopy such as that of soybean (*Glycine max* [L.] Merr.), (2) the ability of eastern black nightshade (Solanum ptycanthum Dun.) to grow in the shade under the crop canopy until late in the season when the crop sheds its leaves, after which it grows vigorously, and (3) the ability of cocklebur (*Xanthium strumarium* L.) to behave and compete like a crop plant, as weed species do in the Spitter and van den Bergh[24] model.

Equation 4 can be corrected for competitive advantages with respect to light by weighting for the relative height of each species.[24] Height growth, of course, is strongly influenced by water and nutrient stress and light quality. Accounting for rainfall and temperature in regression models improved the prediction of control threshold densities (the density where it becomes economical to control the weed) for redroot pigweed (*Amaranthus hybridis* L.) and wild oat (*Avena fatua* L.) in sugarbeet (*Beta vulgaris* L.) fields. However, as correlated parameters are added to regression models, statistical problems associated with accounting for the complex interactions among regression parameters, the environment, and plant processes limit the accuracy of the model.[41]

Through the linking of process models, such as coupling canopy light interception equations with leaf photosynthesis models to give canopy photosynthesis, the mechanisms that control growth and competition can be better understood and quantified, leading to better predictions of crop production systems behavior. The first published physiologically-based crop-weed model, SETSIM,[21] simulates the behavior of foxtail (*Setaria* spp.) in an alfalfa (*Medicago sativa* L.) crop. Carbohydrate flow, storage, and structural root, stem and leaf compartments were determined by rates adjusted for deviations from optimum physiological and/or environmental conditions.

When SETSIM was developed, data on many key aspects of foxtail physiology and growth were lacking. For developing logic describing many of the processes involved, Orwick et al.[21] used their intuition or data from related species. A few parameters were calibrated after testing the model against 5 d of field data. The calibrated version of SETSIM then adequately predicted most aspects of foxtail growth in a second set of data taken over a 25 d period. The authors[21] suggested many ways in which their model might be applied, including the determination of when to apply postemergent herbicides and in the development and testing of new herbicides. Legere and Schreiber[20] used the same approach in their development of logic in AMSIM for predicting redroot pigweed growth.

WEED-CROP[23] is the first published physiologically based model to simulate weed-crop competition. Based on the general crop model SUCROS[42] and the Spitters-van den Bergh[24] model discussed previously, WEED-CROP simulates competition for light and water by stratifying the canopy and root zone and accounting for the relative vertical leaf area and root distributions of each species. Sensitivity analyses of WEED-CROP, using parameters for yellow mustard (*Sinapis arvensis* L.), barnyard grass (*Echinochloa crus galli* L.) and maize (*Zea mays* L.), confirmed the importance of relative height, population density, time of emergence, and newly-emerged seedling size on competitive ability. Spitters and Aerts[23] concluded that C_4 plants have a competitive advantage and that stomatal regulation was crucial for predicting water consumption. McGiffen et al.[43,151] have expanded upon WEED-CROP[37] to develop VELVET for the prediction of soybean and velvetleaf competition.

Spitters[22] simplified WEED-CROP by using site-specific variables for the potential productivity of the crop grown and stand characteristics and ground cover for both the crop and weed. In 5 experiments conducted over 3 years at a range of densities of common lambsquarter (*Chenopodium album* L.), 90% of the variation in yield losses in sugar beet was explained by the model.

IV. MECHANISTIC PHENOLOGY MODELS

As described in the previous section, sensitivity analysis of WEED-CROP[23] confirms the importance of the vertical distribution of leaf area in determining the outcome of weed-crop

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competition. The distribution function used in WEED-CROP, however, was fixed for a given species. If we assume, for example, that the competitive process is actuated by the vertical movement and expansion of leaf area, then a mechanistic model of competition should include the phenological aspects of changes in vertical leaf area distribution. We describe such a phytomer-based approach, following a brief discussion of germination and seedling emergence.

A. GERMINATION

The biology of weed seeds in soil has been reviewed in detail.[44-46] The timing of weed seed germination, with respect to that of the crop, is an important determinant of competition. Seed quality, seed bed characteristics, and rainfall pattern control the relative timing of crop-weed germination. Even under ideal conditions, weed seeds in the soil bank[28] vary in time to germination. The seeds of most weed species also possess the ability to remain dormant, or delay germination until conditions are suitable for germination. Most agronomic weeds evolved as colonizers of unpredictable early successional environments and retain the ability to remain dormant for long periods of time.[47] Germination dynamics, in turn, affect the "critical weed-free period"[7] and determine how the weeds are managed.

Environmental conditions that can end dormancy include chilling, leaching of germination inhibiting compounds from seeds, specific photoperiods, and fluctuating temperatures. In many summer annuals, a chilling requirement to end dormancy may be satisfied during the winter, but emergence does not occur until spring temperatures rise above the germination threshold.[48] A high temperature after-ripening requirement in winter annuals is satisfied during the summer, with fall emergence when temperatures are again optimal for germination.

Thomas[49] found that under light, alternating temperatures stimulated germination for 46 of 112 species studied. For those that germinated, the response varied from an absolute requirement in all seeds of a species for >5°C fluctuations to polymorphic responses where a percentage of the population of a species germinated at a constant temperature and the rest required <5°C fluctuations. Fluctuating temperatures commonly stimulated germination in wetland species as a mechanism for determining when the water table had dropped and irradiance had increased to adequately support establishment. Fluctuating temperatures also act as a depth sensor to stimulate germination in agronomic weeds such as black nightshade, a small-seeded species that must be near the soil surface in order to germinate.[50,51]

Fluctuating temperatures are also used as depth sensing mechanisms for species that form seed banks, or long-term populations of weed seed in the soil.[49] Seeds that are dormant upon dispersal from the mother plant may break dormancy, but be inhibited from germinating by drought or other unfavorable conditions and revert to dormancy.[44] Seeds may persist in the seed bank for several years, cycling from dormant to nondormant as conditions change.

Tillage changes the microsite conditions of individuals in the seedbank, exposing deeply buried seeds to conditions favorable for germination. With regular cultivation and prevention of reseeding, the number of viable weed seeds in the soil decreases, sometimes exponentially.[44] However, while tillage increases the emergence of many weed species, the pattern of time of emergence often remains the same. An exception is prostrate knotweed (*Polygonum aviculare* L.), which emerges earlier with cultivation due to more rapid warming of the soil.[44]

Water must be available to the seed to hydrate the embryo and permit germination to occur. The availability of water to the seed is determined by (1) seed characteristics that influence surface wetting and impede water diffusion, (2) soil properties such as osmotic and matric potential, and (3) seed surface contact with soil particles.[44] Hard-seeded weeds, e.g., velvetleaf, generally do not imbibe even readily available water unless the seed coat is altered to permit water permeability.[52] At low irrigation frequencies, giant foxtail (*Setaria faberi* Herrm.) and velvetleaf emergence increases with decreased soil aggregate size, as the greater number of soil aggregates per seed surface area increases the contact of the seed coat with soil particles.[53] When seeds are inside soil peds, poor soil aeration decreases emergence as irrigation frequency increases.

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In addition to current conditions, the environment while the seed was on the mother plant can affect germination. Baskin and Baskin[54] found that germination of seeds of redroot pigweed (*A. hybridis*) and common lambsquarters (*C. album*) depended on the temperature directly after maturity (after-ripening). After-ripening at high temperatures resulted in the ability to germinate at high temperatures; likewise, the minimum temperature for germination decreased with the after-ripening temperature. Clearly, a single base temperature will not suffice for degree day-based germination models involving these species. Dimorphism has also been noted: seeds from the upper and lower portions of the same fruit in *X. strumarium* can have different germination requirements.[55]

Taylorson and Borthwick[56] showed that light filtered through soybean, corn or tobacco leaves had intensity peaks in the far-red region, regardless of the light source. This filtered light inhibited germination in a number of weed species. Woolley and Stoller[57] found that as little as 6 mm of soil can inhibit light-induced lettuce seed germination. In general, it appears that only seeds near the surface of unshaded soil germinate.

Thornley[58] modeled germination as a series of stages that each member of the population had to pass through sequentially before entering the next stage. Brown and Mayer[59] tested Thornley's approach and were unable to detect evidence of successive developmental stages; they suggested use of simpler sigmoidal functions. Hsu et al.[60] developed a logistic function that includes standard germination indices. Weaver[61] derived a novel function to replace the gamma distribution used in Thornley's approach, and got good fit for tomato (*Lycopersicon esculentum* L.), common lambsquarters, powell amaranth (*A. powellii* S. Wats.), green foxtail (*S. viridis* L.), and eastern black nightshade.

B. VEGETATIVE SPROUTING

The timing of new growth in fleshy taproots, crowns, rhizomes, tubers, corms and bulbs, as well as in buds (axillary, apical, adventitious in roots or shoots) is an important competitive factor in established, overwintering perennials. Of 238 weeds described[62] for the U.S. north central states, 139 were annuals and biennials and 15 were perennials propagated only by seed. Of the remaining perennial weeds, most of which also propagated by seeds, 1 propagated by stem pieces (cactus), 30 by creeping roots or rootstocks (many of which could have been rhizomes) and 44 by rhizomes, stolons, tubers, runners, rooting prostrate branches, and spreading crowns. Nine more overwintered with fleshy taproots. Growth initiation in the spring can involve many of the same environmental factors and physiological mechanisms (photoperiodism, vernalization, nutrition) controlling floral induction, seed growth, and seed germination.[6,63] The horticultural literature offers many well-studied examples of such behavior (e.g., the sprouting of potato tubers[64]); logic for quantifying these processes is urgently needed.

C. SHOOT EMERGENCE

The amount of oil, carbohydrate, or protein in seed or storage organs (bulbs, bulbils, corms, rhizomes, tubers, etc.), as well as the soil impedance (crusting or compaction), affects the shoot emergence rate, along with the many other factors contributing to growth and development. Once again, quantitative logic is needed for describing the soil (structural mechanisms controlling available water, oxygen and temperature) and plant morphogenetic or transport processes involved.

D. LEAF AREA DEVELOPMENT

In an analysis of production models developed to predict the effects of a water stress, de Wit and de Vries[65] stated that "by far the weakest feature of these models is the simulation of assimilate partitioning among organs and the response of plants to water stress in terms of function and morphology. The only morphogenetic aspects that are modeled in a more or less explanatory fashion are the functional balance between shoot and root growth and the development of sink size for growth. Other aspects of partitioning are treated descriptively, such

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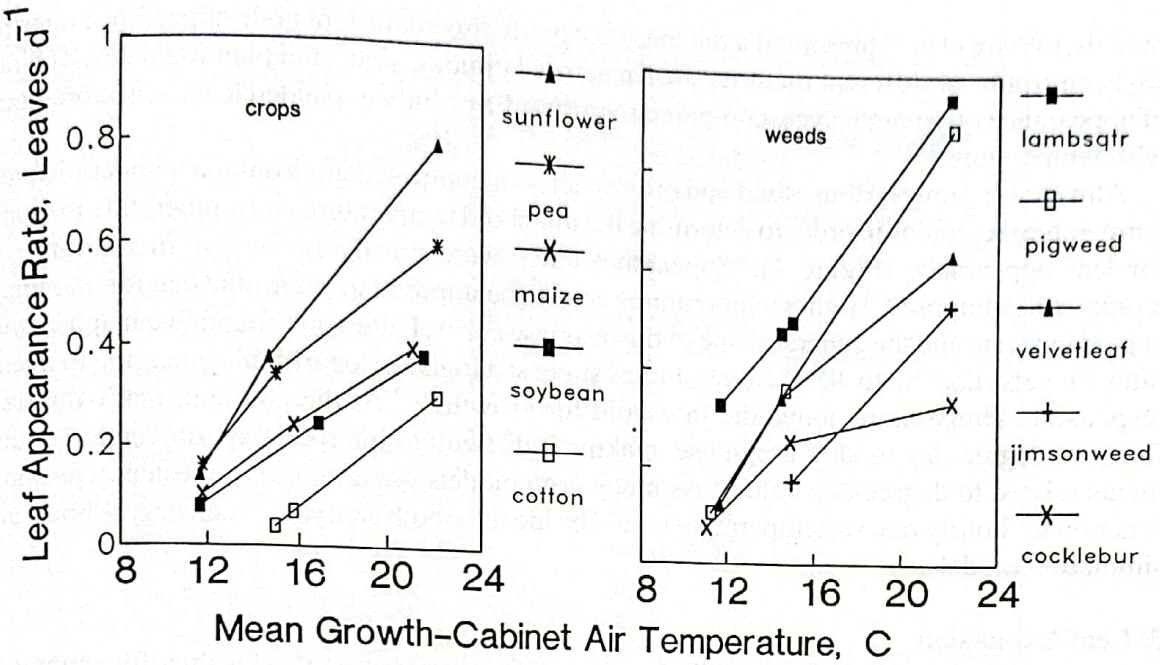

FIGURE 1. Mainstem leaf appearance rates at different mean growth cabinet temperatures for (left) five crop and (right) five weed species. Plants were grown under a 16-h day. From Alm et al.[17]

as distribution patterns in dependence of development stage. This functions rather well in normal conditions but does not deal properly with deviations from the normal pattern when diseases are involved or when weather conditions are extreme. Crop production models are therefore only applied in the predictive mode in situations where it is known that the crop can grow; they are not used to investigate the possibilities in borderline cases. A breakthrough in explanatory modeling of the partitioning of dry matter is badly needed, but can only be expected if there is a renewed interest in morphogenetic problems in the biological sciences." A seminal example of morphogenetic modeling is Kobayashi's[66] model for leaf area expansion and biomass production in sunflower. This phytomer-based model used the well-known Monsi-Saeki model for photosynthetic supply and the carbon requirements of each phytomer segment of the plant for demand.

1. Leaf Initiation

Phytomer growth and development can be defined as beginning with a visible primordial bump, as detected with a dissecting microscope or by other means. Of course, considerable growth and development occur before a primordial bump can be detected. Zur et al.[67] measured leaf primordia, and visible tip and collar (the leaf collar signaling full expansion) appearance rates in maize. They reported both time at a constant temperature and degree days between different events for the same leaf. Primordia appearance rates are needed in corn models to predict the date for tassel initiation and in all growth models for the total number of leaves (TLNO) to be grown. Warrington and Kanemasu[68] also determined the effect of temperature on primordia and ligule production rates in corn. Alm[15] reported a logarithmic relationship between the number of leaves, including the smallest primordium, which cannot be seen without dissection, and the number of visible leaves for field-grown weed species.

2. Leaf Appearance

There are many observations of linear leaf appearance rates under constant temperature.[17,69-71] In recent years, the degree-day approach has gained acceptance as a means of filtering temperature effects from developmental data. (See Cross and Zuber[72] for a review of various

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models.) Wang et al.[73] presented a database for predicting mainstem node appearance rates for soybean strains of different maturity grown across latitudes, years and planting dates. The rate of appearance of young leaves, compared to primordia or fully expanded leaves, is more linear with temperature.[71,72,74,75]

Alm et al.[17] grew various weed and crop species in controlled environments under different temperature regimens in order to determine the threshold temperature and temperature response for leaf appearance (Figure 1). Appearance rates were mostly linear within the range of temperatures imposed. Higher temperatures need to be imposed to determine that for maximum appearance rate and the general shape of the response curve. Patterson[76] found linear appearance rates for velvetleaf up to 40°C. Some studies suggest a logistic (logarithmic changing to linear) response to temperature above the threshold for growth.[68,77] At the moment, many different forms of degree-day models are in use, making it difficult to interpret experimental measurements related to degree-day values. As many crop models use an hourly timestep, a response function for hourly rate vs. temperature would be ideal for both analytical (i.e., degree hour) and simulation models.

3. Leaf Expansion

Leaf area expansion can be described in terms of leaf appearance and is therefore appropriately included in a discussion of vegetative phenology. The importance of the relative rate of leaf area expansion [(1/A)(dA/dt) or R_A] in determining the growth rate of plants,[78-80] as well as competitive ability,[22] has been well demonstrated. Rijsdijk[81] proposed that when the physiological characteristics of growth of weeds and the crop are similar, their growth rates in an even mixture can be written as:

$$G_c = \left[\frac{M_c}{(M_c + M_w)}\right] * G_t \tag{5}$$

and

$$G_w = \left[\frac{M_w}{(M_c + M_w)}\right] * G_t \tag{6}$$

where G = growth rate, M = leaf area index (LAI), c = crop, w = weed, and t = the total stand. Equations 5 and 6 show that the growth of each species in a mixture is proportional to its share of the total canopy leaf area. This kind of linear model should be more accurate when the weeds are more evenly distributed in the crop and when the product of photosynthetically active leaf nitrogen, leaf area, and intercepted light approach a maximum (e.g., at canopy closure).

In addition to playing an important role in competition for light, leaf area could also have a significant part in competition for nutrients and water, in as much as water and nutrient uptake are driven by the root system needed to support transpiration.[22] In order to understand and quantify competition for available resources between two or more plants, leaf area development of each plant must be understood and quantified. Accurate simulation requires not only accounting for how many leaves are produced and how big they are, but also where they develop spatially within the canopy volume. In addition, branching behavior of the plants involved can dramatically alter the total leaf area produced, as well as its spatial distribution[16,40] and effectiveness.[82]

Leaf expansion (or growth — we have thus far discussed only leaf developmental events such as leaf initiation) is temperature dependent,[69,70,75,83-86] although there always is hope that development and growth are affected in the same way and that leaf expansion per phyllochron is constant.[70] Dennett et al.[69] used the Richard's function,[87]

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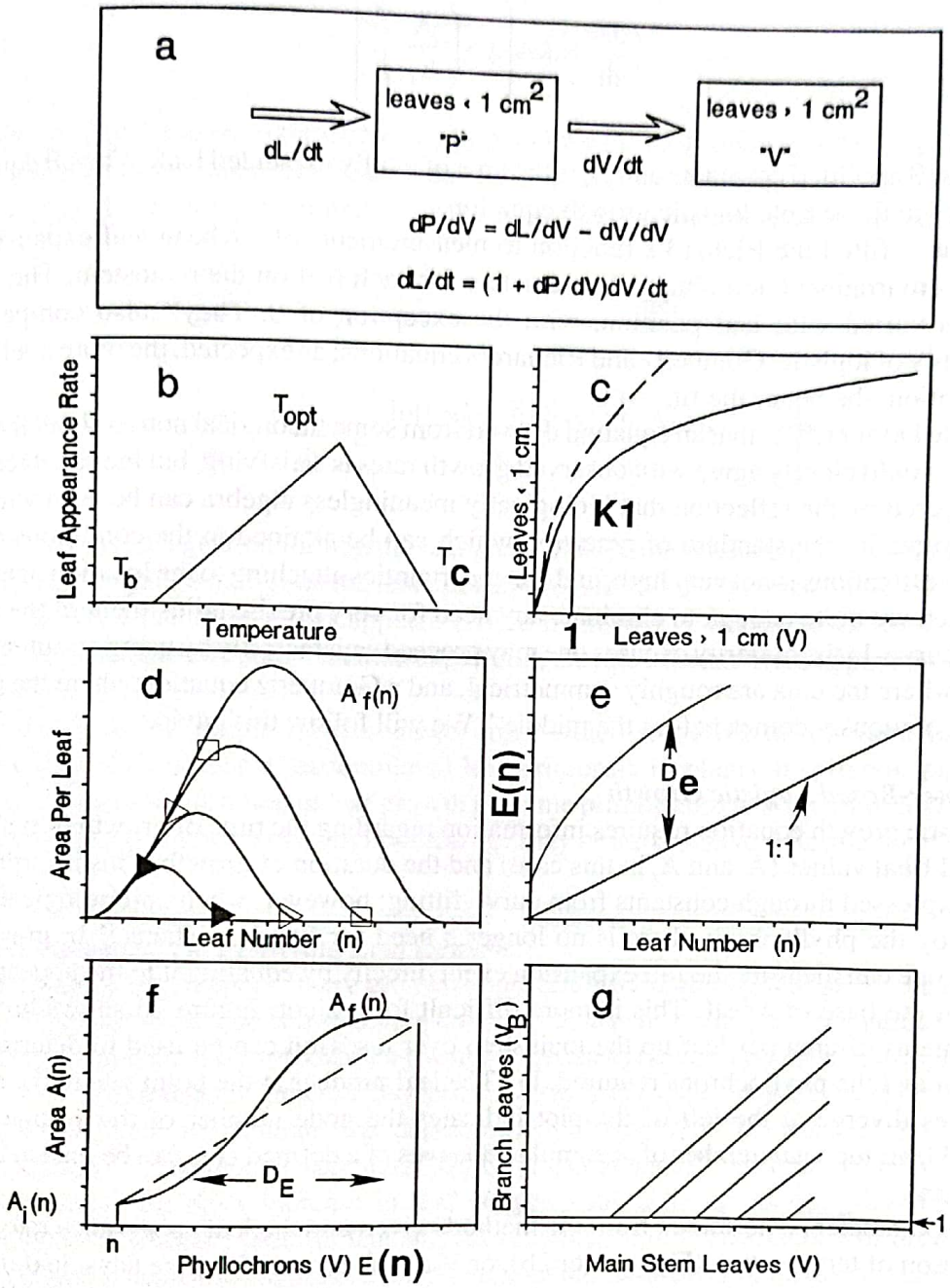

FIGURE 2. A phytomer-based model for leaf expansion. (a) The leaf initiation rate (dL/dt, where L = the total number of accumulated primordia at the shoot apex, including those in the seed) is derived from the appearance rate dV/dt, based on an allometric relationship between the number of leaves less than 1 cm^2 in area (P), visible only after dissection with a microscope, at any given phyllochron index (V, or total accumulated number of leaves greater than 1 cm^2). (b) The leaf appearance rate is assumed to increase linearly with increasing temperature between a base temperature T_b and an optimum temperature T_{opt} and to decrease linearly between the optimum T_{opt} and the ceiling temperature T_c. (c) The relationship between P and V (solid curve) fits the equation $P = k1 + k2\ \ln(V)$. The plastochron index L = P + V (dashed curve) is the sum of P and the 1:1 line. (d) Area per leaf A(n) vs. leaf number n. The phyllochron index when leaf n is fully expanded, or E(n), is determined by the point of divergence of a given curve from the final leaf area curve $A_f(n)$. (e) E(n), or the value of V when leaf n stops expanding, vs. leaf number n, represented by the point symbols on the abscissa and the curves in (d), respectively. The duration of expansion (in phyllochrons), D_e, is the distance between the E(n) curve and the 1:1 line, or E(n) – n. (f) Simple logistic (solid line) or linear (dashed line) growth is completely determined by the final area $A_f(n)$, and the duration of expansion, expressed in phyllochrons, $D_e(n)$. (g) The appearance of primary branch leaves V_B vs. the appearance of mainstem leaves V. The slope of any given line is the branch:mainstem ratio for leaf appearance, or dV_B/dV. From Alm.[15]

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$$\frac{dA}{dt} = kA\left[1-\left(\frac{A}{A_f}\right)^{\frac{1}{\theta}}\right] \quad (7)$$

where k and θ are fitted constants and A_f is the area of a fully expanded leaf. When θ equals one this reduces to the simple logistic growth equation.

Cao et al.[88] fitted the Richard's function to measurements of soybean leaf expansion in a controlled environment and obtained parameters for each leaf on the mainstem. The various parameters varied with leaf position, with the exception of θ. They[88] also compared the predictability of logistic, Gompertz and Richard's equations; as expected, the more coefficients in the equation, the better the fit.

To quote Dorner,[89] "...that an equation derived from some theoretical notion about the nature of growth should closely agree with observed growth rates is satisfying, but the satisfaction has to be tempered by the reflection that biologically meaningless algebra can be used with equal success. In reality the standard of precision which can be attained in the conditions of most growth investigations is not very high, and the uncertainties attaching to the location of the point of inflection are quite enough to eliminate any need for very precise adjustment of the form of the fitted curve. In the majority of cases one may proceed satisfactorily by using an autocatalytic equation where the data are roughly symmetrical, and a Gompertz equation where the point of inflection obviously comes before the middle." We will follow this advice.

a. Phytomer-Based Logistic Growth

A logistic growth equation requires information regarding the time of growth initiation, the initial and final values (A_i and A_f in this case) and the duration of growth. This information is usually expressed through constants from curve-fitting; however, when chronological time is replaced by the phyllochron, there is no longer a need for fitted constants.[15] In grasses, for example, one can measure the full expansion event directly by equating it to the appearance of a collar at the base of a leaf. This is more difficult for a dicot; Figure 2d shows how serial measurements of area per leaf up the mainstem over a season can be used to determine full expansion and the phyllochrons required, D_e. The leaf number at the point where the area per leaf curves diverge at the left of the plot indicates the node number of the youngest fully expanded leaf; the total number of accumulated leaves of a defined area can be read at the right of the plots.

Using parameters determined from the methods given and the leaf appearance rate (dV/dt) as a function of temperature (Figure 1 or 2b), or V as a function of degree days, leaf initiation and appearance can be predicted for a growing season. From Figure 2d, area per leaf (A_n) at each node (n) can be used with the duration of expansion data (Figure 2e) to predict leaf area expansion, assuming no branching.

Figure 2f depicts the growth curve of a typical expanding leaf, "n", at the "n^{th}" node of the plant, given an initial area, ($A_{i,n}$) such as 100 mm^2, the maximum area ($A_{f,n}$), and the duration for expansion ($D_{e,n}$). The average leaf expansion rate on a chronological time base is

$$\frac{dA_n}{dt} = \left[\frac{\left(A_{f,n} - A_{i,n}\right)}{D_{e,n}}\right]\frac{dV}{dt} \quad (8)$$

This equation may be adequate for predicting whole plant area over time; it might be improved by reducing D_e and delaying expansion with the linear part of the expansion curve (Figure 2f and McNaughton[79]). For more detail, one might use a general logistic growth equation:[21]

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$$A_n = \frac{A_{f,n}}{\left[1 + b\left(e^{-k[V-n]}\right)\right]} \tag{9}$$

where the time unit has been replaced by phyllochrons (V – n), since leaf "n" appeared at V = n. At V = n, the exponential term equals 1, and $b = [(A_{f,n}/A_{i,n}) - 1]$. When $A_n = A_{f,n}/2$, $k = 2[\ln((A_{f,n} - A_{i,n})/A_{i,n})/D_{e,n}]$. Omitting the notation for each leaf (n), the first derivative of Equation 9 is

$$\frac{dA}{dV} = \frac{kA(A_f - A)}{A_f} \qquad \text{and}$$

$$\frac{dA}{dt} = \left(\frac{dV}{dt}\right) 2\left[\frac{\ln\left((A_f - A_i)/A_i\right)}{D_e}\right]\left[\frac{A(A_f - A)}{A_f}\right] \tag{10}$$

Equation 10 is a rate equation for logistic leaf growth given the final area, A_f, the initial area, A_i, the duration of expansion, D_e, and the leaf appearance rate dV/dt. Of course, it will be integrated over D_e phyllochrons after a leaf appears on the mainstem or branch until the final area is attained. To predict whole plant leaf area expansion, the rate of branch leaf appearance, dV_B/dV, needs to be known.[153]

The search is for simple measurements from which to derive all of these parameters. Dissecting for the number of accumulated leaf primordia in plants at different phyllochron stages gave values for duration of leaf growth from the primordium to a 100 mm^2 leaf. Areas for a few leaves on a plant of known phyllochron age may be sufficient to describe A or A_f vs. node number.

b. Other Approaches to Modeling Leaf Growth

As delineated by Stapper,[90] there are two approaches to modeling leaf area: expansion and growth. "The first technique computes the daily increase in leaf area from temperature and rate of plant development, and is modified by water stress and plant competition" through resource balance and physiological process models. Carbon and water balance models should be sufficiently detailed to simulate the dependence of alleviation of water stress on recent photoassimilate.[91] "The second technique," according to Stapper,[90] "computes the daily increase in leaf area from the daily increase in leaf weight using a (temperature, growth stage, and possibly light-dependent) specific leaf weight function." Some modelers will argue that the second method is more mechanistic, but both require the same physiological data and will have approximately the same degree of cybernetic connectance (or, approximately, feedback; see Gardner and Ashby[92] for a discussion of connectance). The true difference between approaches lies in the entry point to the system: which comes first, the area or weight? Whisler et al.[93] argued that calculating the potential expansion as a function of temperature is more mechanistic. In this case, leaf area expansion becomes an explicit phenological function.

Spitters and Aerts[23] and McGiffen et al.[43] modeled leaf expansion after emergence as an exponential function of temperature, with a stress reduction factor. At a species- specific developmental state, computation of the increase in leaf area switched from this approach to one based upon the increase in leaf dry weight and the specific leaf weight.

Charles-Edwards[94] described a model of leaf expansion based on a biophysical analogy, in which eight state variables represent classes of chemicals in the leaf. His model described various qualitative aspects of leaf growth in a physiologically meaningful way. The main assumption of the model is that the rate of cell wall synthesis is positively related to the rate of water uptake, which in turn is positively related to the amount of labile carbohydrate and

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FIGURE 3. The appearance of primary branch leaves V_B vs. that of mainstem leaves, see Figure 2(g). A new leaf was counted when it had 1 cm² area or more. The slope of a line through the points for a particular branch is dV_B/dt and the horizontal distance between two successive lines at the V_B = 1 cm² intercept is dV/dB, or phyllochrons per branch leaf. The data were collected from widely spaced plants early in the 1988 growing season.

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negatively related to the amount of cell wall. The negative feedback of the cell wall on water uptake is a power function. Recently, however, the validity of the assumed effect of turgor (linear response above a yield threshold, depending on wall extensibility) on cell growth[95,96] has been questioned.[97] Shackel et al.[97] found cell expansion to be independent of turgor on a short time scale. A physical/chemical model of leaf expansion is, at this time, probably of less value in a community model than is a phenological description.

4. Internode Growth

Hesketh et al., in their chapter on stem growth, reviewed various aspects of stem physiology. The stem is extremely important for modeling the materials balance in weeds. Weeds have not been exposed to directed selection pressure for fruit yield and invest more in stem parts than do most crops. In addition, internode elongation rates determine the vertical height of the leaf area and hence the pattern of interference.

Internode elongation in dicots is a complex process.[98] Gibberellins are frequently implicated in internode elongation[99] and Maksymowych et al.[100] found the relative internode elongation rates to double in response to GA_3. Partial shading will usually increase elongation. Growth in internode length is generally logistic.[66] A phyllochron-based logistic model, such as that described for leaf area expansion, may be appropriate for internode elongation. However, the dynamics of materials cost for an internode of a plant growing in a mixed stand is far from clear; the competitive ability in overtopping dicots such as velvetleaf and jimsonweed (*Datura stramonium* L.) may well be determined by the ability to meet the internode material demand. Petiole elongation[101] also determines the final shape of the canopy.

5. Branching

The idealized relationship between the phyllochron index of a branch module (a module is made up of successive phytomers produced by the same meristem), V_B, and that of the mainstem, V, is shown for a plant with axial branch appearance proceeding acropetally (up from the ground) (Figure 2g). The slopes are the ratio of the appearance rate of the branches to that of the mainstem, or dV_B/dV. Figure 3 shows data for redroot pigweed and common lambsquarter. A new branch with a 100 mm^2 leaf appears at node "n" (line "n" in Figure 3) when $V_{B,n} = 1$ for V_B regressed against V. From the relationship (Figure 2c) between the accumulated primordia plus mainstem leaves (P + V), or L, and V, the value of V when branch n was initiated can be derived, given the number of plastochrons between initiation of the mainstem leaf and the initiation of its first axillary leaf, k_4. If the relationship between P and V is the same for branches as for the mainstem, the value of V when this event occurs can be obtained from Figure 2c.

Once the branch is initiated, this approach assumes that branch leaf primordia are initiated at a constant rate per phyllochron until the first leaf appears. Tomlinson[102] distinguishes two developmental subdivisions of branching as either *sylleptic* or *proleptic*. The former refers to branching without a period of dormancy, while the latter refers to a preliminary inhibition of the branch meristem after it has been initiated. The technique discussed previously describes apparent sylleptic development, although a dormancy period could easily be added. The only way to distinguish the two paths is through frequent dissections over the growth period. Dissections combined with environmental treatments would be extremely valuable; there are clearly windows when branch development is more susceptible to control by the environment.[103,104]

The rate of branch appearance is simply

$$\frac{dB}{dt} = \frac{\left(\frac{dV}{dt}\right)}{\left(\frac{dV}{dB}\right)} \qquad (11)$$

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where dV/dB is the average horizontal distance (phyllochrons) between two $V_B = 1$ intercepts in Figure 2g or Figure 3, and a branch appears as B passes each positive integer. The rate of branch leaf appearance, or dV_B/dt is

$$\frac{dV_B}{dt} = \left(\frac{dV_B}{dV}\right)\left(\frac{dV}{dt}\right) \quad (12)$$

This logic was generally derived for dicots with axial branching behavior and a single dominant apical meristem. Apparent dichotymous branching, such as occurs in the nightshades (Solanaceae) are "remarkable example(s) of the early replacement of a parent shoot by a daughter shoot, which itself is rapidly replaced by a granddaughter shoot, and so on; the whole scheme is complicated by shoot and leaf fusions."[105] This shoot-leaf fusion is obvious on examination of the long ridges formed where petiol and stem fuse. The overtaking of the main axis by the lateral meristems, though not always obvious (some mainstems are a series of sympodia), could be modeled as an event, much like the branching event equations derived previously.

An alternative approach to modeling branch development is through cohort analysis. Bazzaz and Harper[106] pioneered the technique of grouping phytomers into cohorts and analyzing the plant as a population. Maillette[107] presented a matrix model of the bud population of a silver birch whereby the shape of the tree was explained by the distribution of developmental rates. This approach may have some merit in a crop-weed situation. However, we feel that an explicit morphological analysis presents less in the way of conceptual and mathematical barriers, although computational demands will become large for simulation modeling at the community level.

There are numerous articles by ecologists and foresters on branch angles and algorithms that give rise to certain patterns.[108-110] As far as we know, the logic outlined previously is the first derivation of dicot branching behavior on a phyllochron basis. A similar effort was made for barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) by Kirby et al.,[111] assuming that the leaf emergence rate was the same for all shoots. Their observations, however, showed that the later tillers had slower emergence rates than the earlier tillers. Such slowing of branch development could be due to the approach of reproductive development; alternatively, it could be an inherent part of the vegetative pattern. Board and Settimi[112] found branch development in determinate soybean plants to be determined by the time between R1 and R5, which was reduced by short days, before or after flowering. Mainstem leaf number was not affected by photoperiod.[112] Alm[15] found differences in branch leaf appearance rate for different branches on a number of weed species, but the ratio of branch leaf appearance to mainstem leaf appearance was conspicuously close to one for widely spaced plants.

E. SEXUAL REPRODUCTION AND SENESCENCE

Weed species have been used in many classic studies on the effect of photoperiod and temperature on floral bud initiation and development and seed growth,[3,5,36,113] with phenological events for bud or seed growth defined in great detail. Similar information was available for crop plants before crop models were developed. However, for predicting crop reproductive phenology, new field and controlled environment research had to be done to properly quantify the effects of the environment on the schedule of events. We have begun to accumulate information for some weeds,[16] but not enough to develop a flowering model (e.g., soybean[73]). Most of the literature describes studies using discrete daylengths and controlled environment manipulations that are difficult to relate to field conditions. Wang et al.[73] demonstrated how phenological

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measurements on crops planted at different dates and latitudes can be used to generate cultivar-specific temperature × photoperiod functions. Constable and Rose[114] found an effect of the rate of change of daylength on flowering through regression analysis. Similar work is required for weed species and races. There are some field studies, such as a 15 year phenological record of pasture plants,[115] that may help in developing field models. Undoubtedly, a detailed review of the methods and flowering times in interference studies could yield valuable information.

The reduction of vegetative growth that accompanies flowering is commonly attributed to remobilization of nutrients for fruit and seed growth. Thus, to accurately model leaf area development, materials balance data is required for weed reproductive as well as vegetative organs. However, the nutrient-scavenger hypothesis apparently does not hold for soybean[116,117] or common cocklebur.[117] Begonia et al.[118] used source-sink manipulations and various cultural conditions to study factors affecting leaf duration in soybean and maize, and suggested a genetic difference among cultivars. Similar studies should be performed on weeds from various locations in order to detect any senescence ecotypes.

F. ASEXUAL REPRODUCTION

Kigel and Koller[6] reviewed the many aspects of asexual reproductive behavior in weeds in great detail, using proper morphological terminology. They discussed some of the associated competitive advantages and disadvantages (or strategies), compared to seed production. The importance of disconnection from the mother plant and dispersal by cultivation was discussed in detail. They also described how secondary horizontal roots can grow some distance from the primary root before turning down and sending up a shoot from an adventitious bud. This bud appears just before the bend, and other horizontal roots capable of repeating this process are sent out from the new shoot. Their discussion of tuber, rhizome, stolon, and bulb morphology and physiology is the best we found in our literature search. They,[6] Vince-Prue,[63] and Trewavis[119] discussed how photoperiod, temperature and nutrition interact to control the initiation, growth and development, dormancy, and sprouting of such organs. These factors interact in much the same way to control sexual reproduction and germination.

G. ROOT DEVELOPMENT

Klepper et al.[120] developed a model for root development in wheat based on the phyllochron. There are few such efforts for crops[121] and none for weeds. The ecological literature holds data concerning root:shoot ratios as a function of the environment; some of the species studied are agronomically important weeds. Most root studies involve growing plants in containers. Competition within and between plants is increased when a container is used. When possible, field root studies, however gross, should be used to develop model logic and obtain parameters. Geddes et al.[122] found that the roots of intraspecific cocklebur and of interspecific cocklebur plus soybean plants explored a larger volume of soil for water than did intraspecific soybean plants, but rooting depths were about the same; however, Monks et al.[123] found that up to the 9 week stage, seedlings of cocklebur rooted deeper than soybean seedlings. Soybeans competing with velvetleaf extract water from deeper in the soil than weed-free soybeans.[124] Further studies are needed to determine the rate of depth exploration and the plasticity of the rate as determined by soil-weather-ecotype interactions in important weed species.

The production of root adventitious buds leading to new shoots is reviewed in some detail by Kigel and Koller.[6]

H. MODELING THE EFFECTS OF COMPETITION ON PHENOLOGY

Competition affects phenology through individual organs and meristems. For example, the effects of shading are the integrated effects of changes in light quantity and quality received by individual phytomers. Branch modules are initially net sinks to the whole plant or branch; however, at some time they become autonomous. Autonomy may be correlated with vascular

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development, but there are substantial variations in the relationship between mainstem and branch vascular connections, even within a species.[125] The question of whether developmental control is local or at the whole plant level is too general to be useful. Clearly, some behavioral responses of phytomers are due to the time-integrated sum of effects of their local environments while others are due to that of the whole plant.

When a new axillary branch is still a sink, the carbon balance of the module with which the branch is associated can influence the fate of such a sink. Charles-Edwards[94] formalized a hypothesis whereby meristems require a critical minimum assimilate for growth, and hence the number of meristems should correlate with the net assimilation per unit ground area.

There are many studies linking increased far-red levels in the local light environment to increased internode elongation[54] and axillary meristem development.[126] Ballare et al.[127] demonstrated increased internode elongation in (*Chenopodium allium*), *Sinapis alba*, and *Datura ferox*, after exposure to far-red light imposed with reflecting mirrors. They[54] suggested that sensitivity to the far-red:red (FR:R) ratio in the local light environment serves as an early warning signal for approaching competition. Casal and Smith[128] found that a red pulse given via optical fibers to the internode of *S. alba* neutralized the far-red effect on internode elongation. They[128] also found that a far-red pulse at the internode was followed by a short-lived enhanced elongation, while a far-red pulse on the leaf resulted in an extended period of internode elongation. Begonia and Aldrich[126] found that broad band-pass acetate filters, which increased the far-red light received by soybean nodes, reduced the production of fruiting branches.

Although phytochrome may be involved in determining whether an axillary bud is released, the branch is not immediately autonomous. Continued development must initially be supported by whole plant assimilate, gradually changing to a self-supporting module. Growth regulators apparently mediate control of the flow of materials to and from individual organs. Physiological coordination is usually localized,[26] however, because of the way organs are interconnected by vascular tissue. Vascular connections seem to constrain where nutrients flow, rather than how fast.[117]

There are apparently three decisions being made during the time course of branch development: (1) whether or not to release the axillary bud, (2) whether or not to continue supporting the (sink) branch, and (3) whether the autonomous branch can support itself or should abort. The first decision is apparently the result of interactions between the response of the individual phytomer and the whole plant to their environments; the second is probably a whole plant response and the third is determined at the individual module level. This is clearly a simplistic view, but such logic lays the foundation for interfacing materials balance models with phytomer-based phenology to yield a mechanistic model of competition.

Patterson[129] and Berkowitz[130] reviewed the effects of the environment on weed physiology, growth, and competitiveness; they found little data at the phytomer level or on a thermal time basis. In addition, the degree to which a weed infestation can be accurately measured and defined for model initialization is a major limitation to predictability. Frazee and Stoller[131] developed regression equations relating the height of several weed seedlings to the number of mainstem leaves. These relationships should be useful when developmental stages are required for model initialization and only height data are available; competitive interactions would be minimal during the early diagnostic stages. This problem of description of the weeds for model input deserves much attention.

In the following sections, we highlight the physiological ecology of a few selected weed species, with emphasis on how this literature can aid in the development of phytomer-based phenology models. The merits of a crop-weed competition model, however, will be judged according to how well selected output variables agree with a measured quantity in a field experiment. Just as finite scientific knowledge and technological constraints limit the nature of the processes one can consider in a particular modeling project, practical limits on experimental validation determine the degree to which a model can ever be tested. Put simply, detail in the system definition (state variable structure) should agree with detail in data collection. There is

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no point in modeling growth at the phytomer level if validation is performed at the whole plant level.

1. Common Cocklebur and Velvetleaf

Common cocklebur is an aggressive weed that can, in contrast to shade-intolerant species, maintain robust leaves deep down in the soybean crop canopy throughout the growing season.[15,132] Regnier et al.[132] found that both soybeans and common cocklebur reduce the amount of soluble protein in the leaves when grown under reduced irradiance. They suggested that this is a response made to conserve energy (as dark respiration rates were correlated with protein concentration) and may allow maintenance of these lower leaves. Velvetleaf, conversely, aborts lower leaves early, with an apparent strategy of overtopping its neighbors. Increase in internode length and inhibition of axillary branching is usually much more pronounced for velvetleaf than for cocklebur when growing in a soybean crop.

Full season velvetleaf competition reduces soybean leaf, stem, root, pod, and seed dry matter, as well as LAI, pod number, and seed yield.[133] Competitive effects are due to reduced yields of individual soybean plants and not reduced stands.[134] Velvetleaf reduced soybean dry weight twice as much as either green or yellow foxtail (*Setaria viridis* and *Glauca* L.)[135] and was more competitive with soybeans than venice mallow or prickly sida.[136]

Velvetleaf adapts morphologically and physiologically to the light intensity of its environment. As described, velvetleaf adjusts the rate of growth of height with plant density and competing species present[18] to maintain leaves above the crop canopy, denying competitors direct sunlight.[40]

The response of velvetleaf to temperature and photoperiod has implications for crop competition. Velvetleaf gains a competitive advantage over cotton after early season cool periods by rapid recovery from chilling.[137] In Arkansas, the apparent photoperiod sensitivity of velvetleaf reduces full-season competitive effects from a 27% yield reduction for velvetleaf emerging with soybeans in mid-May to a 14% yield reduction when velvetleaf emerges with soybeans planted one month later.

Drought reduces velvetleaf, cotton, and spurred anoda: height, leaf number, leaf area, total dry weight, stomatal conductance, transpiration, net assimilation rate, leaf duration, and biomass partitioned into leaf and stem.[138] The time at which weed dry weight and leaf area equals cotton is delayed during drought, suggesting a competitive advantage for cotton; as described earlier, the reverse is apparently true for common cocklebur and soybeans. Velvetleaf is more sensitive to drought than soybeans; velvetleaf photosynthetic rate drops more sharply after water stress, and soybeans can extract water from deeper in the soil profile.[124]

2. Redroot Pigweed and Common Lambsquarters

These two weeds are discussed together because of their common feature: a dense canopy of relatively horizontal, small leaves. The branching and leaf area development algorithms derived earlier require a state variable for leaf area at each leaf. This does not present a problem for weeds such as velvetleaf and common cocklebur, which have comparatively few, large leaves. Pigweed and lambsquarters, however, have many leaves on secondary and tertiary branches. We have dealt with this problem by lumping all leaf area that arises at a primary branch node.[15]

These two weeds have been the subject of many photosynthetic studies because they have similar niches and growth habits but contrasting photosynthetic pathways. Flint and Patterson[139] found pigweed to be a better competitor at higher temperatures, a typical characteristic of C_4 plants. The observation that pigweed caused less interference with soybeans than foxtail suggests that the photosynthetic pathway may not be as important as the growth form and habit in determining competitiveness. Many of the most agronomically important weeds do not possess the C_4 pathway.[129]

Duke and Hunt[140] found that pigweed (and velvetleaf) plants had larger stems and more axillary branching when grown under metal halide than under fluorescent-incandescent lights.

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Growth chamber and glass house competition experiments should therefore be extrapolated with caution. Bhaskar and Vyas[141] found common lambsquarters to be a good competitor for nitrogen and phosphorous, but wheat to be better at accumulating potassium.

3. The Solanaceae: Apparent Dichotymous Branching

A complex of four *Solanum* weed species have been historically identified as black nightshade: American black nightshade (*S. americanum* Mill.), black nightshade (*S. nigrum* L.), Eastern black nightshade (*S. ptycanthum* Dun.), and hairy nightshade (*S. sarrachoides*).[142] All four species may grow either prostrate or erect, which presents a new problem for canopy volume logic. The black nightshades produce juicy berries that often rupture if harvested with beans, reducing crop quality by staining and causing seeds and soil particles to cling to beans.

Crop losses have been reported due to Eastern black nightshade interference. Yield loss in tomatoes rises dramatically as Eastern black nightshade density increases, leveling off at densities greater than four plants per meter.[143] At the same weed densities, yield reduction for full-season competition is three times greater for field-seeded tomatoes than for transplants.[61]

Sporadic emergence of the nightshades throughout the growing season results from a seed dormancy controlled by environmental factors. Near Prosser, WA, two emergence peaks of Eastern black and black nightshade occurred in spring and late summer.[142] Fresh seeds were dormant, but black nightshade seed buried the previous year and retrieved from April through July had 100% germination; dormancy sharply increased for seed retrieved from August through October. Diurnal temperature fluctuations and red light end dormancy in black nightshade,[50] a response postulated to restrict germination to seeds in canopy light gaps and close to the soil surface.[47]

Meyers[144] found that Eastern black nightshade survives under crop canopies by efficient use of low light intensity. Eastern black nightshade, velvetleaf, common lambsquarters, tumble pigweed (*Amaranthus albus* L.), and soybean all respond to reduced irradiance by reducing respiration rate, decreasing root/shoot weight, and increasing leaf area ratio, but the response is most pronounced for Eastern black nightshade. Eastern black nightshade plants enduring shady conditions can quickly take advantage of increased light due to leaf shedding in a senescing crop canopy and can rapidly produce a large number of fruits and seed before the crop is harvested.

Quakenbush and Andersen[145] found that soybean competition reduces Eastern black nightshade duration of flowering, berry production, and seedling survivorship. Time to reach the two leaf stage is the same for intra- or interspecific Eastern black nightshade planted up to 6 weeks after soybeans, but is greater if nightshade emerges later. Soybean interference increases time to flowering by several weeks. The authors[145] also found that mid-season defoliation decreased the time required to reach either the two-leaf or the reproductive stage.

Both the nightshades and jimsonweed display apparent dichotymous branching. As mentioned earlier, the lateral meristems overtake the apical meristem. This presents problems, not only for branching logic, but for branching geometry. The height of a given leaf is not a simple calculation based on a single branch angle and a sum of subtending internode lengths.

Jimsonweed is much larger than the nightshades and presents problems in a soybean crop for different reasons. Late season shade contributed to most of the interference with the soybean crop at low weed density, indicating competition for light.[146] As described, jimsonweed does not maintain its lower leaves under competition with soybean; this phenomenon was related to the lack of ability to lower the dark respiration rate under shade.

V. VERTICAL INTEGRATION

It is management practice to strive to maintain the population parameters of the crop at a relatively constant level. In a well-managed annual crop, a known number of seeds are planted in a precise arrangement and depth, and to ensure that they emerge over a narrow time span, the

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organisms that might interfere with the life cycle of the crop are controlled, the life cycle is over a discrete period from planting to harvest, and seeds are removed from the field at harvest. Crop models thus ignore many population parameters and use values, such as planting density, as inputs, with an emphasis on predicting how an average plant behaves.

The factors that determine the number of weeds and the timing of their life cycles are not as consistent. A useful competition model must deal with these inconsistencies. In addition, different flushes of weeds may have different phenological behavior.

Many areas of modeling weed phenology need to be considered, and there is a great need for studies at the phytomer level. Much remains to be determined, particularly the dynamics of the mechanisms controlling vertical leaf area distribution, as well as the flowering-seed growth and vegetative reproductive behavior of many weed species in agricultural ecosystems. The reviews[2,3,5,6,45] on how plants adapt or acclimate to stress (see Table 1), including frosts and freezing, need to be greatly expanded, with some emphasis on how the adaptation or acclimation processes enhance the competitive ability of the plant, as well as on the role of phenology and its physiological basis.[63,147] Some weed behavioral characteristics enhancing competitiveness, which were not discussed by the reviewers mentioned, include the following:

1. The production of many small seeds to take advantage of gaps in a crop stand.
2. Shade tolerance, or endurance in shade, and the ability to resume rapid growth when the overtopping canopy loses its leaves.
3. Storage of large C and N reserves in winter, drought or shade enduring vegetative storage organs, which can sprout and grow rapidly under more favorable conditions at the proper time.
4. Extend internodes, orient shoot toward a light gap, delay flowering, or fruit set, expand larger leaves, redistribute N to new growth, to overtop a short crop, or to compete successfully with a tall crop.
5. Rapid expansion of leaf surfaces and extension of stems and roots.

This and other lists need to be developed further, with examples. As indicated in Table 1, plants have many options to deploy to survive abiotic stresses, to compete with other plants or organisms, to adapt or acclimate to climate change, and to produce more biomass. How a particular species or race does this cannot always be anticipated, and may well be hidden in its genetic makeup until revealed by climate change.

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